The Triassic Lycopsids *Pleuromeia* and *Annalepis*: Relationships, Evolution, and Origin

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ABSTRACT.—Two kinds of isoetalean lycopsids widely prevailed in the Triassic, the *Pleuromeia*-type and the *Annalepis*-type, the latter including a plexus of closely related genera. Comparative studies using new macromorphological and ultrastructural data suggest that both genera are interconnected and closely related to *Isoetes*. Morever they suggest that *Annalepis* is probably ancestral to *Isoetes*, via *Isoetites*. Besides several of the morphological and ultrastructural features of the Triassic lycopsids and *Isoetes* also appear to be present in some of the most ancient lycopsids, suggesting that the lineage including the modern Isoetales has a very remote origin.

The lycopsids have the longest evolutionary history of any vascular land plants, covering about 400 million years and spanning every geological period from the Siluro-Devonian to the present. Although their structural diversity has decreased considerably since their peak in the Carboniferous, they were still widespread in the Triassic of both hemispheres. However the Mesozoic lycopsids were not arborescent like many of the Carboniferous ones but rather consisted of slender, herbaceous or pseudoherbaceous plants having an unbranched habit. Two kinds of lycopsids widely prevailed in the Triassic, the *Pleuromeia*-type and the *Annalepis*-type, the latter including a plexus of closely related genera, which are all regarded as belonging to the isoetalean lycopsids (Pigg, 1992).

Pleuromeia Corda was long regarded as one of the intermediates between the Carboniferous arborescent lepidodendrids and living *Isoetes* and thus thought to be part of a reduction series (Solms-Laubach, 1899; Potonié, 1904; Mägdefrau, 1931). This concept was questionned by Jennings (1975) who noticed that the lycopsids with a cormose rhizomorph already existed in the Upper Devonian, long before the lepidodendrids with a dichotomously branched *Stigmaria* rooting system. However DiMichele and Bateman (1996) also suggested, on cladistic foundations, that the isoetaleans evolved from the lepidodendraleans and that the bilateral condition emerged from the radial one in the Devonian. Nevertheless Bateman (1994, 1996) recognized that the precise relationships between both groups are ambiguous.

The comparative study of *Pleuromeia* and *Annalepis* presented here, using new macromorphological and ultrastructural data, shows that these Triassic isoetalean lycopsids appear closely related to *Isoetes* and that *Annalepis* seems to be closer than *Pleuromeia* to the living genus. Moreover this study consti-

tutes a new basis for comparison with other lycopsids and for evaluating and possibly clarifying the relationship between the isoetaleans and the lepidodendrids.

THE TRIASSIC LYCOPSID *PLEUROMEIA*: COMPARATIVE STUDY

Although the lycopsid *Pleuromeia* Corda was long regarded as being phylogenetically highly significant, it was never estimated at its true value because many characteristics of this widespread Triassic genus were not known with enough accuracy. The progress in knowlege of its rhizomorphs, growth habit, reproductive organs and spores now allows to propose a comprehensive comparative analysis of this outstanding genus.

THE RHIZOMORPH OF *PLEUROMEIA*.—As in the other rhizomorphic lycopsids (Bateman 1996), the rooting organ of *Pleuromeia* has proven to be, phylogenetically, highly informative since it shows many similarities with that of *Isoetes*, suggesting that these lycopsids are closely related. The reinvestigation and morphological analysis of several fairly well-preserved rhizomorphs of *P. sternbergii* (Münster) Corda in light of new data on *Isoetes* permit us to demonstrate the structural and developmental correspondence between both. Thus most of the features of the rhizomorph of *P. sternbergii* can be interpreted in terms of those of the living genus (Grauvogel-Stamm, 1993).

Like the rhizomorph of *Isoetes*, that of *Pleuromeia* is lobed and shows a bilaterally symmetrical furrow system, when seen from below (Figs.1a-f). The four-lobed rhizomorph of *P. sternbergii* has a central furrow bifurcating distally into two peripheral furrows which run along the midline of the lobes and extend upward into their extremities (Fig. 1c). Its roots have the same structure as those of *Isoetes* and *Stigmaria*. As in *Isoetes* but unlike *Stigmaria*, they are arranged on both sides of the furrows according to two intersecting row systems, one roughly parallel to the furrows (series) and the other diverging from them at a relatively high angle (orthostichies) (Fig. 1f). In the two-lobed rhizomorph of *P. epicharis* Wang and Wang (1990) from the Lower Triassic of China, the roots are also arranged in series and orthostichies on both sides of the straight furrow, as in the two-lobed rhizomorph of *Isoetes* (Figs.1a,b,e). This bilateral arrangement suggests that the roots were produced as in the living genus. That is, they are produced by a basal linear root-producing meristem underlying the lobed stele and running parallel to the furrow, and the roots emerged at the furrows and were progressively displaced by continued meristematic activity. The lobing of the rhizomorph developed in relation to this meristem and this process of root production. However the difference in cortical development in *Pleuromeia* and *Isoetes* resulted in a difference in lobe and furrow arrangement (Figs.1a-d). Indeed in *Isoetes* where the cortex is strongly developed, the peripheral furrows of a four-lobed rhizomorph seem to run between the lobes (Fig. 1d). In fact, the correct developmental correspondence requires comparing the lobes of *Pleuromeia* with those of the root-bearing stele in *Isoetes*, without its cortical lobes. Observations on the diameter
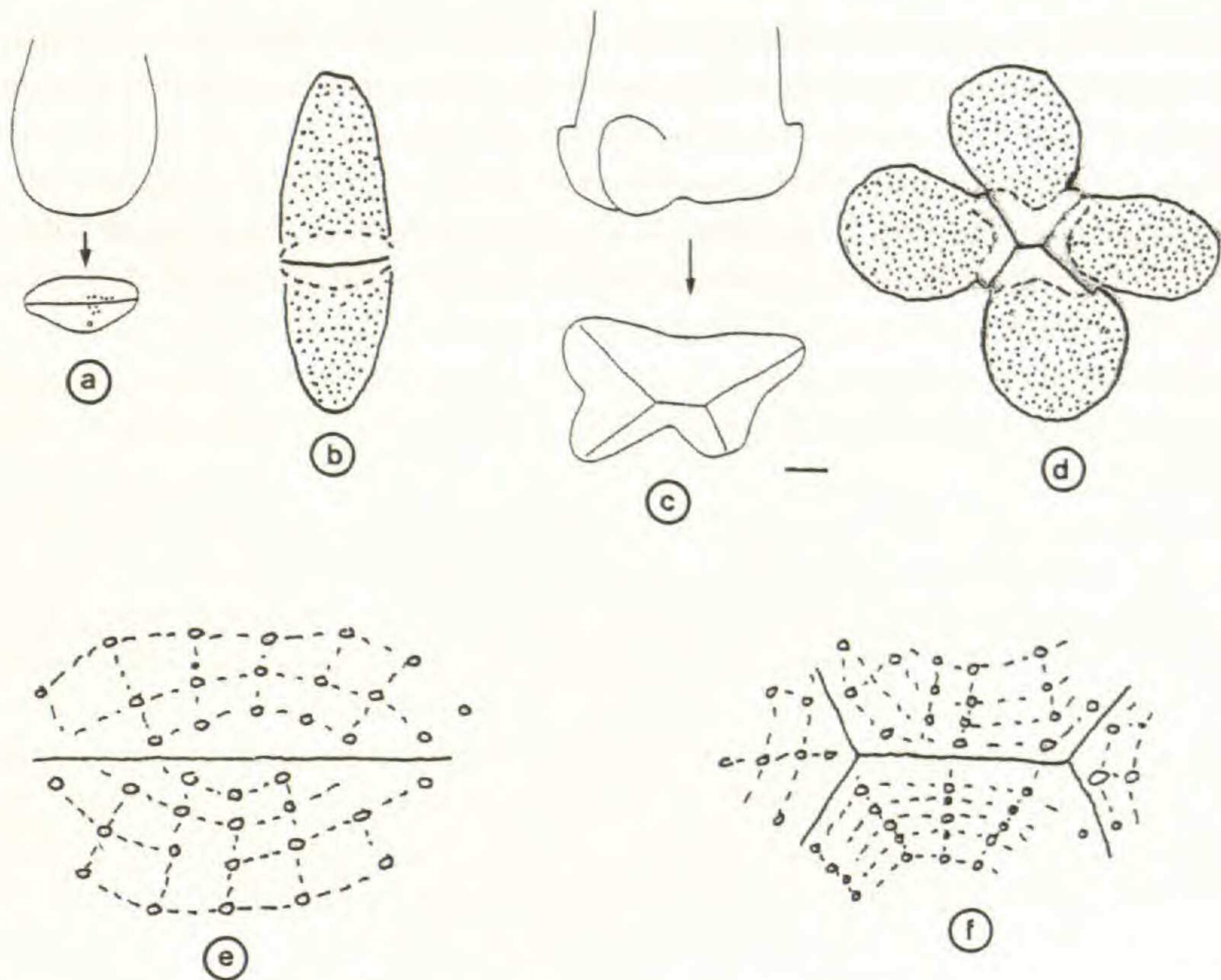
FIG. 1. Comparative morphology of the rhizomorphs of *Pleuromeia* and *Isoetes*. a—Side-view (above) and underside view (below) of a two-lobed rhizomorph of *Pleuromeia*, such as those of *P. epicharis* (Wang and Wang, 1990) or *P. sanxiaensis* (Meng, 1995) from the Triassic of China. b—Cross section of a two-lobed rhizomorph of *Isoetes* at the level of the basal meristem and furrow (inferred from Karrfalt and Eggert, 1977). This rhizomorph has a straight furrow like the two-lobed rhizomorph of *Pleuromeia* in Fig. 1a, but its two lobes (stippled) are more developed due to the great cortex production. c—Side-view (above) and underside view (below) of a four-lobed rhizomorph of *Pleuromeia*, like that of *P. sternbergii* (Grauvogel-Stamm, 1993) or *P. rossica* (Neuburg, 1960; Dobruskina, 1982). The bilaterally-symmetrical furrow system consists of a central furrow bifurcating at both extremities into two peripheral furrows which run along the midline of the lobes. d—Cross section of a four-lobed rhizomorph of *Isoetes* at the level of the meristem and furrow system (inferred from Karrfalt and Eggert, 1977). The furrow-system is similar to that of *Pleuromeia* in Fig. 1c, but the high cortex production resulted in the development of cortical lobes (stippled) between those of the root-bearing stele. Thus the correct developmental correspondence requires comparing the lobes of *Pleuromeia* with those of the root-bearing stele in *Isoetes* (cortical protrusions excluded). e—Root arrangement on both sides of the straight furrow in a two-lobed rhizomorph of *Pleuromeia* or *Isoetes*. The root scars are arranged according to two intersecting row systems, one roughly parallel to the furrow (series) and the other diverging at a relatively high angle (orthostichies) (modified from Karrfalt and Eggert, 1978). f—Root arrangement in series and orthostichies on both sides of the bifurcated furrow system in the four-lobed rhizomorphs of *Pleuromeia* or *Isoetes* (modified from Karrfalt and Eggert, 1978).

of the root scars of *P. sternbergii* in relation to their place on the rhizomorph demonstrate that root production proceeded in an acropetal direction as in *Isoetes*. The significant increase of the root scar diameter from youngest to oldest (also observed in *P. epicharis*, unpublished observations, L. G.-S.), their numerical increase with the aging and thickening of the rhizomorph, and the maintenance of their arrangement give evidence for long retention of the roots,

possibly their persistence throughout the life of the plant as in *Selaginella*. This is unlike *Isoetes* in which the roots are regularly lost and replaced. The sequence of root initiation, the orientation of the root traces inside the lobes and thus the direction of their emergence and the marked lengthening of the peripheral furrows which occurred during ontogeny show how the rhizomorph of *Pleuromeia* developed laterally to the detriment of its downward growth. This new restatement of the structure of the rhizomorph of *P. sternbergii* and the comparative study with the living *Isoetes* accurately emphasizes the numerous points of structural and developmental correspondence between these plants.

Fossil lycopsids with a cormose rhizomorph that is furrowed, lobed and bilaterally symmetrical are rather rare in the literature. Besides *P. sternbergii*, such a rhizomorph has been described in *P. rossica* Neuburg from the Lower Triassic of the Russian platform (Neuburg, 1960; Dobruskina, 1982) and *P. epicharis* from the Lower Triassic of China (Wand and Wang, 1990). The rhizomorphs of *P. sternbergii* and *P. rossica* are four-lobed and quite similar (Fig. 1c). In contrast, the rhizomorph of *P. epicharis* which is two-lobed, shows a straight, unbranched furrow (Fig. 1a). Also *P. sanxiaensis* Meng (1995) from the early Middle Triassic of South China has a two-lobed rhizomorph. Besides *Pleuromeia*, three other lycopsids with lobed, furrowed, and bilaterally symmetrical rhizomorphs have been described: *Protostigmaria eggertiana* Jennings from the Lower Carboniferous of Virginia, USA (Jennings, 1975; Jennings et al., 1983), *Nathostianella* Glaessner and Rao (1955) from the Lower Cretaceous of South Australia, and *Nathorstiana* Mägdefrau from the Lower Cretaceous of Germany (Karrfalt, 1984). Unlike *P. sternbergii*, they have no prominent lobes. In the lobed rooting organ of *Cylomeia* White (1981) from the early Triassic of Australia, no furrows have ever been mentioned and the other data are too imprecise to interpret this feature. In *Chaloneria cormosa* Pigg and Rothwell from the Pennsylvanian of North America, which is said to have a rounded, slightly lobed, and bilaterally symmetrical cormose rooting organ (Pigg and Rothwell, 1979; 1983; Pigg, 1992), the furrow system has not been mentioned and the root arrangement has not been described. The lobe and furrow system of *Chaloneria* was not fully documented because of the incomplete preservation of cortical tissue on plant bases of available specimens (Pigg, personnal communication, 1999). Among the cormose lycopsids, there are others in which the rhizomorph is radially or nearly radially symmetrical, such as *Paurodendron fraiponti* Fry from the Upper Pennsylvanian of Ohio, USA (Rothwell and Erwin, 1985) and *Oxroadia gracilis* Alvin from the Lower Carboniferous of Scotland (Stewart and Rothwell, 1993). Moreover, several other cormose lycopsids clearly lack an extensive branched rooting system but are not well enough preserved to permit a precise study of their rhizomorph. These are *Lepidosigillaria whitei* Kräusel and Weyland, *Cyclostigma kiltorkense* Haughton, possibly *Eospermatopteris erianus* (Dawson) Goldring from the Devonian (see Pigg, 1992, 2001), *Bodeodendron* Wagner/*Sporangiostrobus feistmantelii* (Feitmantel) Němejc from the Late Stephanian of Spain (Wagner, 1989) and *Clevelandodendron ohioensis* Chitaley and Pigg (1996) from the

Late Devonian of Ohio, USA. In all of the cormose lycopsids cited above, the structure of the rhizomorph, its development, and its root arrangement are not known with as much precision as in species of *Pleuromeia*.

The bilaterally symmetrical cormose rhizomorphs of *Pleuromeia* and *Isoetes* seem to differ greatly from the radially symmetrical stigmarian rooting organs of the lepidodendrids which are dichotomously branched and in which the roots are helically arranged. However, Rothwell and Erwin (1985) demonstrated that the radially and bilaterally symmetrical rhizomorphs are homologous and that they are merely growth variations rather than indicators of two major lines within the rhizomorphic lycopsids as suggested earlier by Jennings (1975) and Jennings et al. (1983). These homologies were the basis for including both the Isoetales and Lepidodendrales of the traditional classifications in the rhizomorphic or isoetalean clade (Rothwell and Erwin, 1985; Stewart and Rothwell, 1993; DiMichele and Bateman, 1996).

GROWTH HABIT AND REPRODUCTIVE ORGANS OF *PLEUROMEIA*.—The similarity in rhizomorphic structure which suggests a close relationship between *Pleuromeia* and *Isoetes* strongly contrasts with the differences in growth habit and reproductive structure of these plants. In *Pleuromeia* (Fig. 2c-g) the sterile leaves differ greatly from the fertile ones which form a well defined cone at the apex of the stem whereas in *Isoetes* (Fig. 2h, 7d), the fertile and sterile leaves are alike and do not form a cone (Jermy, 1990). However such differences seem to be frequent in related lycopsids. The genera *Polysporia* Newberry and *Chaloneria* which belong to the Chaloneriaceae and produce morphologically similar microspores and megaspores, are characterized by well-defined terminal cones in *Polysporia* (Grauvogel-Stamm and Langiaux, 1995) and by fertile zones in *Chaloneria* in which the sporophylls resemble the sterile leaves (Pigg and Rothwell, 1983). Likewise, in the extant genera *Phylloglossum* and *Huperzia* of the Lycopodiaceae which produce comparable spores, there is a compact strobilus in the first genus while the second genus has either fertile zones or compact strobili (Øllgaard, 1990).

All the *Pleuromeia* species, which have been discussed by Dobruskina (1985) and Pigg (1992), consist of unbranched plants having basal cormose rhizomorphs and terminal, well defined cones. The sizes of the plants are rather variable but many species are relatively small. Even among specimens of *P. sternbergii* from the type-locality (Bernburg, Germany) for which Mägdefrau (1931) indicated a height of 2–2.5 m, there are fertile specimens which only reach 23 cm (Fig. 2d) (Grauvogel-Stamm, 1999). Those from the Eifel in Germany (Fig. 2c) are 1–1.5 m tall (Mader, 1990; Fuchs et al., 1991). *Pleuromeia rossica* from the Lower Triassic of Russia was no more than 1 m high (Neuburg, 1960) and *P. jiaochengensis* Wang and Wang (1982) from the Lower Triassic of China usually reached 20–30 cm high, sometimes 50 cm (Fig. 2e). Recently, several new species have been described from the early Middle Triassic of southern China (Meng, 1995,1996) which consist of plants mostly 50 cm high. However, *P. marginulata* Meng (Fig. 2f) includes specimens more
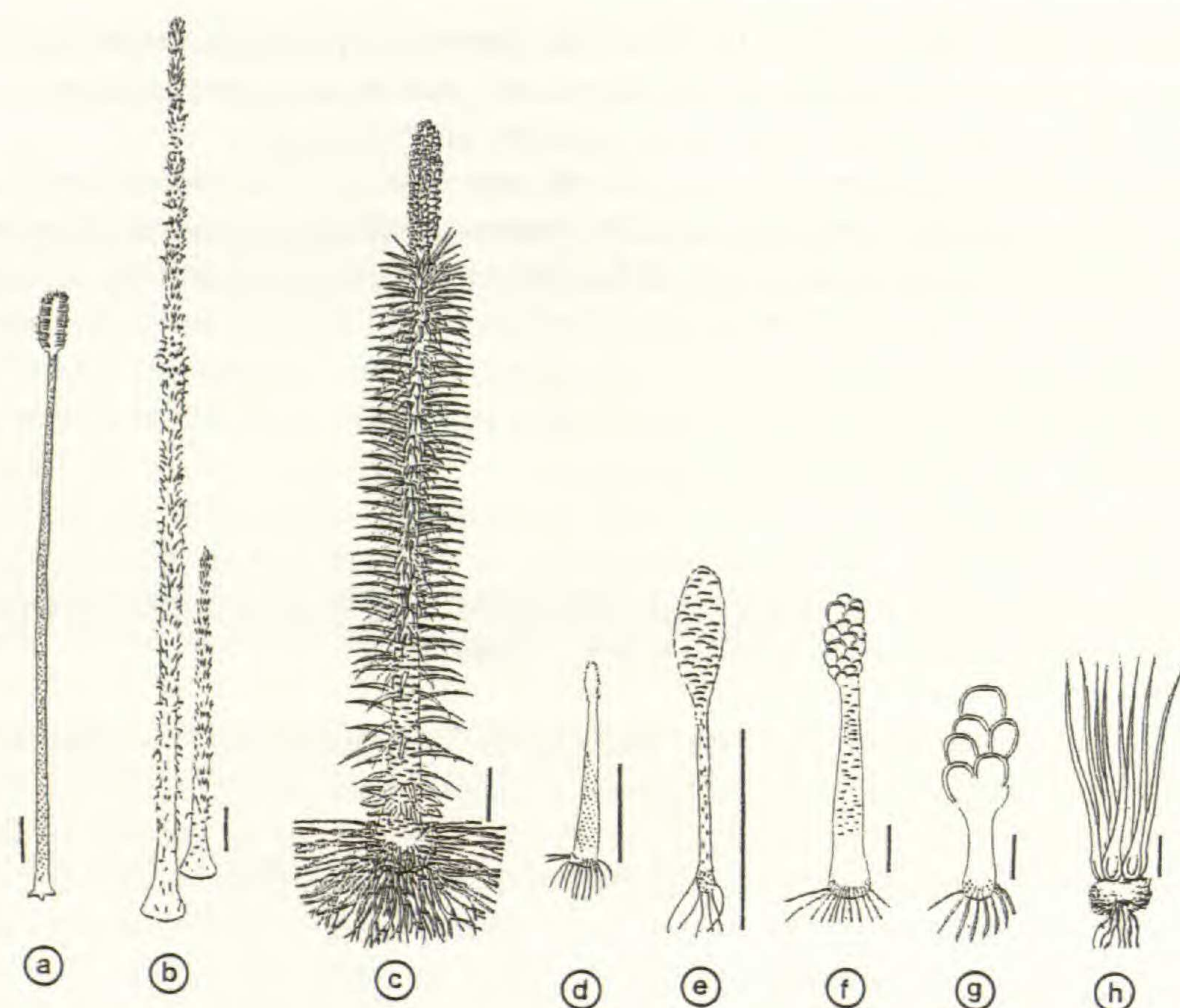
FIG. 2. Comparative growth habit of the Paleozoic and Triassic *Pleuromeia*-like lycopsids and the extant *Isoetes*. (scale-bar = 10 cm, except in Fig. 1g,h = 1 cm). a—*Clevelandodendron ohioensis;* Devonian of Ohio, USA (redrawn from Chitaley and Pigg, 1996). b—*Chaloneria cormosa;* Pennsylvanian of North America (redrawn from Pigg and Rothwell,1983). c—*Pleuromeia sternbergii;* Lower Triassic (Olenekian) of the Eifel, Germany (from Fuchs et al., 1991). d—*P. sternbergii* from the Lower Triassic of Bernburg, the type-locality, (reconstructed after the illustrations of Bischof, 1853, Figs.1,2). e—*P. jiaochengensis;* Lower Triassic (Induan) of Shanxi, China (redrawn from Wang and Wang, 1982). f—*P. marginulata;* early Middle Triassic (Anisian) of South China (reconstructed after the illustrations of Meng, 1995: Pl.1 fig.l and Meng, 1996: Pl.1 fig 1). g—*P. sanxiaensis;* early Middle Triassic (Anisian) of South China (reconstructed after the illustrations of Meng, 1995, 1996, Pl.1 Fig. 9). h—*Isoetes brochoni,* showing leaves 3–7 cm long (redrawn from Motelay, 1893).

than 1 m high. In contrast, *P. sanxiensis* Meng is only 5 cm tall, with a 2,5 cm long cone (Fig. 2g).

The trunk of *Pleuromeia* is usually devoid of leaves but is covered with helically arranged leaf scars. However some of the specimens of *P. sternbergii* from Eifel had trunks covered with leaves (Fig. 2c). These leaves have a strong midvein and, according to Mägdefrau (1931), they were succulent and contain transverse ridges extending perpendicularly on both sides of the midvein. As suggested by Grauvogel-Stamm (1999, Fig. 4), these transverse ridges might correspond to air chambers, as in *Isoetes* and *Isoetites phyllophilla* Skog, Dilcher and Potter (1992). However this feature requires further investigation.

Cone size is variable in *Pleuromeia*. According to Mägdefrau (1931), the cone of *P. sternbergii* reached 20 cm long. However, other cones of that species

are only 5 cm long (Bischof, 1853, Figs.1,2; Grauvogel-Stamm, 1999). Likewise according to Mägdefrau (1931), the cones were monosporangiate, containing either microspores or megaspores. Nevertheless, the small cone figured by Bischof (1853) is clearly bisporangiate (Grauvogel-Stamm and Lugardon, in preparation). Its microsporophylls and megasporophylls are inter-mixed as in *P. rossica* (Neuburg, 1960). The cones of *P. sternbergii* appear to be mono- or bisporangiate depending perhaps on the size and the age of the plants. The two cones on which Mägdefrau (1931) relied were rather large whereas that of Bischof (1853) is small. In *Isoetes* too, the size of the plants has an influence on the production of microsporophylls and/or megasporophylls (Williams, 1943).

The sporophylls of the different *Pleuromeia* species show a remarkable similarity in shape and structure since they consist of a circular to oval lamina and a large, globose sporangium which covers nearly all of the adaxial surface (Figs.3a-j). Distally, the margin has a slight notch or a tiny pointed tip at the apex. The ligule is attached immediately distal to the sporangia and is often obvious in the apical border of the sporophylls (Figs.3a,c,d,h-j). Trabeculae similar to those of *Isoetes* have also been observed in the sporangia of several species. According to Snigirevskaya (1989), the sporophylls of *Pleuromeia* are similar to *Isoetes* leaves having lost their distal sterile portion. Indeed, as suggested by this author, they had a tip which was longer than usually depicted but which dried and decayed in maturing cones. However, examination by one of us (L.G.-S.) of sporophylls of *P. sternbergii* and *P. rossica* in side view shows that they have a tip extending from the lamina without direction change and that this tip is a little longer than the border of the sporophylls in face view (Grauvogel-Stamm, 1999), but never as long as suggested by Snigirevskaja (1989).

Lycopsids with the same growth habit as *Pleuromeia* already existed in the Paleozoic: *Clevelandodendron ohioensis* Chitaley and Pigg (1996) from the Late Devonian of Ohio, USA and *Chaloneria cormosa* Pigg and Rothwell (1983) from the Pennsylvanian of North America. *Clevelandodendron ohioensis* consists of 1.25 m tall unbranched plants covered with helically arranged leaf scars, and possessing a well defined bisporangiate cone containing trilete microspores and megaspores (Fig. 2a). Its partially preserved rhizomorph is said to bear "thick appendages". *Chaloneria cormosa* is also unbranched, and is 2 m tall with a bilaterally symmetrical cormose rhizomorph (Fig. 2b). Its reproductive organs consist of a terminal fertile zone up to 21 cm long, with alternating megasporangial and microsporangial regions resembling the sterile ones.

Meyen (1987) has suggested that *Pleuromeia* evolved from *Chaloneria*, and Stewart and Rothwell (1993) state: "*Chaloneria* seems to bridge the gap between the Upper Devonian treelike lycopsids with their cormose rhizomorphs and the cormose Triassic *Pleuromeia*". The discovery of *Clevelandodendron ohioensis* may indicate that a lineage comprising *Pleuromeia*-like plants already existed in the Late Devonian and was contemporaneous with the beginning of the radiation of arborescent lepidodendrids. This suggests that the di-
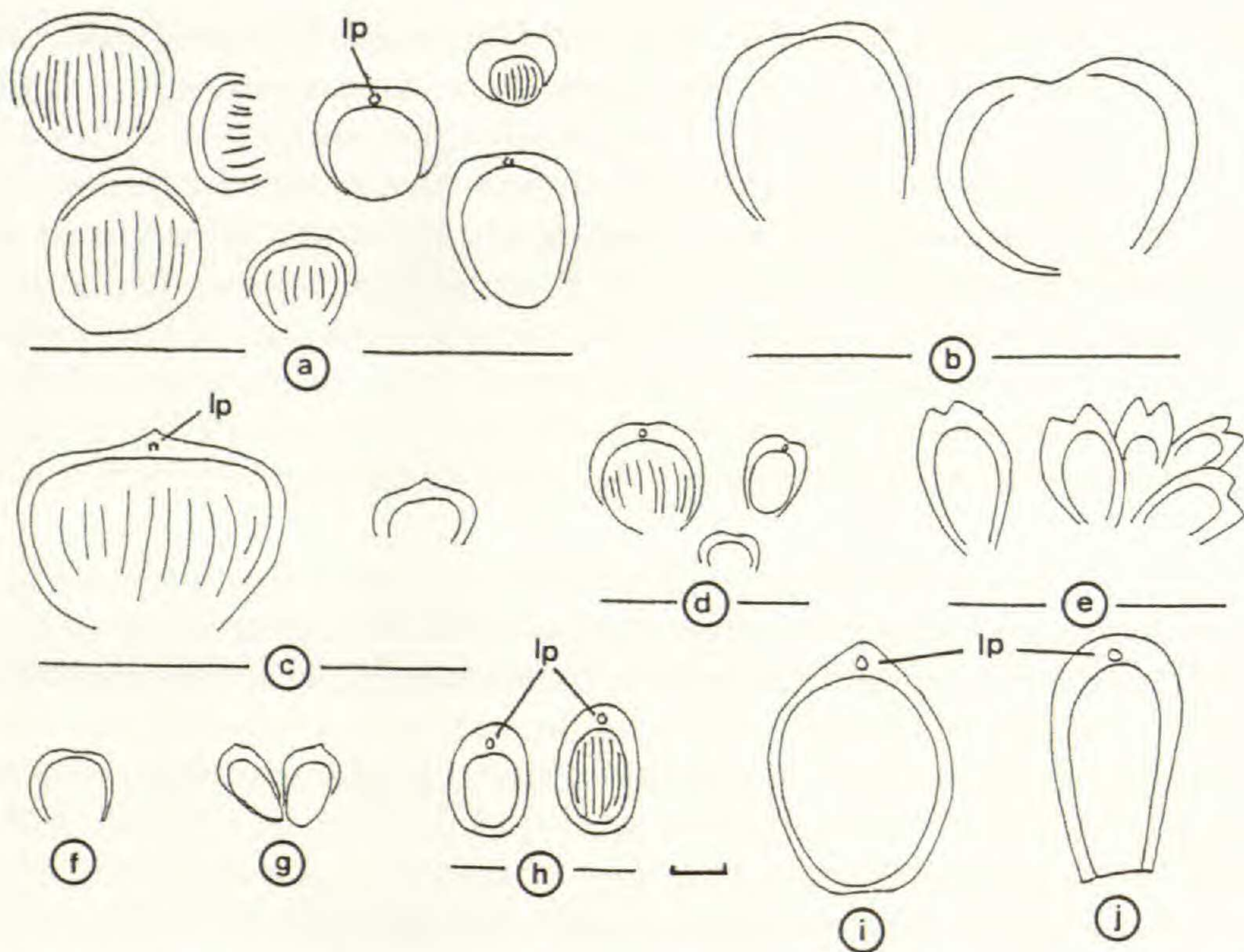
FIG. 3. Comparative shape of the sporophylls in *Pleuromeia*. Note the globose sporangium occupying most of the upper surface; note also the ligular pit (lp) distal to the sporangium, often visible in the narrow apical border of the sporophyll. (scale-bar, between h and i = 1cm). a—*P. sternbergii*; Lower Triassic of Germany (redrawn from Solms-Laubach, 1899; Potonié, 1904). b—*P.altinis*; Lower Triassic of North China (redrawn from Wang and Wang, 1989). c—*P. sternbergii*; Lower Triassic of North China (redrawn from Wang and Wang, 1989). d—*P. rossica*; Lower Triassic of Russia (redrawn from Neuburg, 1960; Dobruskina, 1982). e—*P. epicharis*; Lower Triassic of North China (redrawn from Wang and Wang, 1989, 1990). f—*P. patriformis*; Lower Triassic of North China (redrawn from Wang and Wang, 1989). g—*P. jiaochengensis*; Lower Triassic of North China (redrawn from Wang and Wang, 1982). h—*P. sanxiaensis*; early Middle Triassic of South China (redrawn from Meng, 1995, Fig. 3b,c). i—*P. marginulata*; early Middle Triassic of South China (redrawn from Meng, 1995, Fig. 3a). j—*P. hunanensis*; early Middle Triassic of South China (redrawn from Meng, 1995, Fig. 3d).

versification within the Isoetales was well established prior to the Carboniferous (Chitaley and Pigg, 1996). It may also question the statement of Di-Michele and Bateman (1996) which suggests that the isoetalean line evolved from the lepidodendrids.

THE SPORES OF *PLEUROMEIA*.—Like the structure of the rhizomorphs, the ultrastructure of the spores of *Pleuromeia* appears to be phylogenetically informative, suggesting a close affinity with *Isoetes*.

The microspores of both genera, especially, show many ultrastructural similarities (Lugardon et al., 1997, 1999). This is all the more noteworthy since *Isoetes* microspores have a rather large number of distinctive characteristics which clearly differentiate them from all the other extant spore types, as stressed below. In order to underscore the similarities in ultrastructure and

correspondences of the homologous walls of *Pleuromeia* and *Isoetes* microspores, a description of both is given hereafter (Fig. 4).

Isoetes microspores are monolete spores easily recognizable, through light microscope, by an apparently bipartite sporoderm consisting of an ovoid, unadorned inner part wrapped in a wide, thicker, usually slightly ornamented outer part (Fig. 4a). The inner part is generally regarded as the exospore in morphological studies, while the outer part is variously interpreted and termed (perine, sexine. . .). TEM studies (Lugardon, 1973, 1980) have shown that these microspores possess three distinct aceto-resistant walls (Fig. 4b). The innermost one, which really represents the exospore, is a thin, almost plain-surfaced, bilayered wall that is characterized mainly by its aperture and by special areas of the wall called "laminated zones" (= "zones pluristrates" in the initial description of Lugardon, 1973). The aperture is distinguished by a simple reduction of the exospore thickness, without any other special modification. The laminated zones are small, appreciably thickened areas of the exospore arranged on both sides of the aperture, in which the exospore inner layer is tangentially cleft into several irregularly segmented laminae. The middle wall, that is called "para-exospore", consists of interconnected elements composing a spongy layer which is detached from the exospore all around the spores except in some points of the lateral regions of the proximal face; moreover this wall forms a high projection, usually divided apically into two lips, above the aperture. The outermost wall, which is termed perispore, is a rather thick, complex wall closely applied to the para-exospore surface. Ontogenetical fine studies (Lugardon, 1990; Tryon and Lugardon, 1991) showed that the para-exospore elements develop at the same time as the exospore outer layer, through simultaneous accumulation of the same sporopollenin on the exospore inner layer and on the tenuous framework of the para-exospore that is formed very early in the course of sporogenesis. Moreover, these studies showed that the perispore develops after the para-exospore and exospore completion, with materials of different chemical nature, like the typical perispore of homoporous fern spores (it is generally admitted that a genuine perispore is formed only in pteridophytes having a plasmodial tapetum; nevertheless, TEM studies proved that, besides the microspores of recent Isoetaceae, those of a number of Selaginellaceae, as well as the spores of rather numerous Lycopodiaceae, have a perispore comparable to that of the fern spores, although the lycopsids possess a secretory tapetum; Lugardon, 1990). Thus the wide sporoderm outer part of *Isoetes* microspores comprises two quite distinct components, i.e an uncommon structure, the para-exospore, that is ontogenetically related to the exospore, and a veritable perispore.

The microspores of *Pleuromeia* are trilete and rounded or rounded-triangular in equatorial outline (Fig. 4c). The morphological studies achieved with light and scanning electron microscopes (Neuburg, 1960; Yaroshenko, 1975) showed that these microspores have an outer envelope largely separated from a much thinner inner part often called inner body. The outer envelope appears spongy and faintly ornamented. The inner body is roughly smooth-surfaced and reveals under the light microscope, especially in specimens having lost
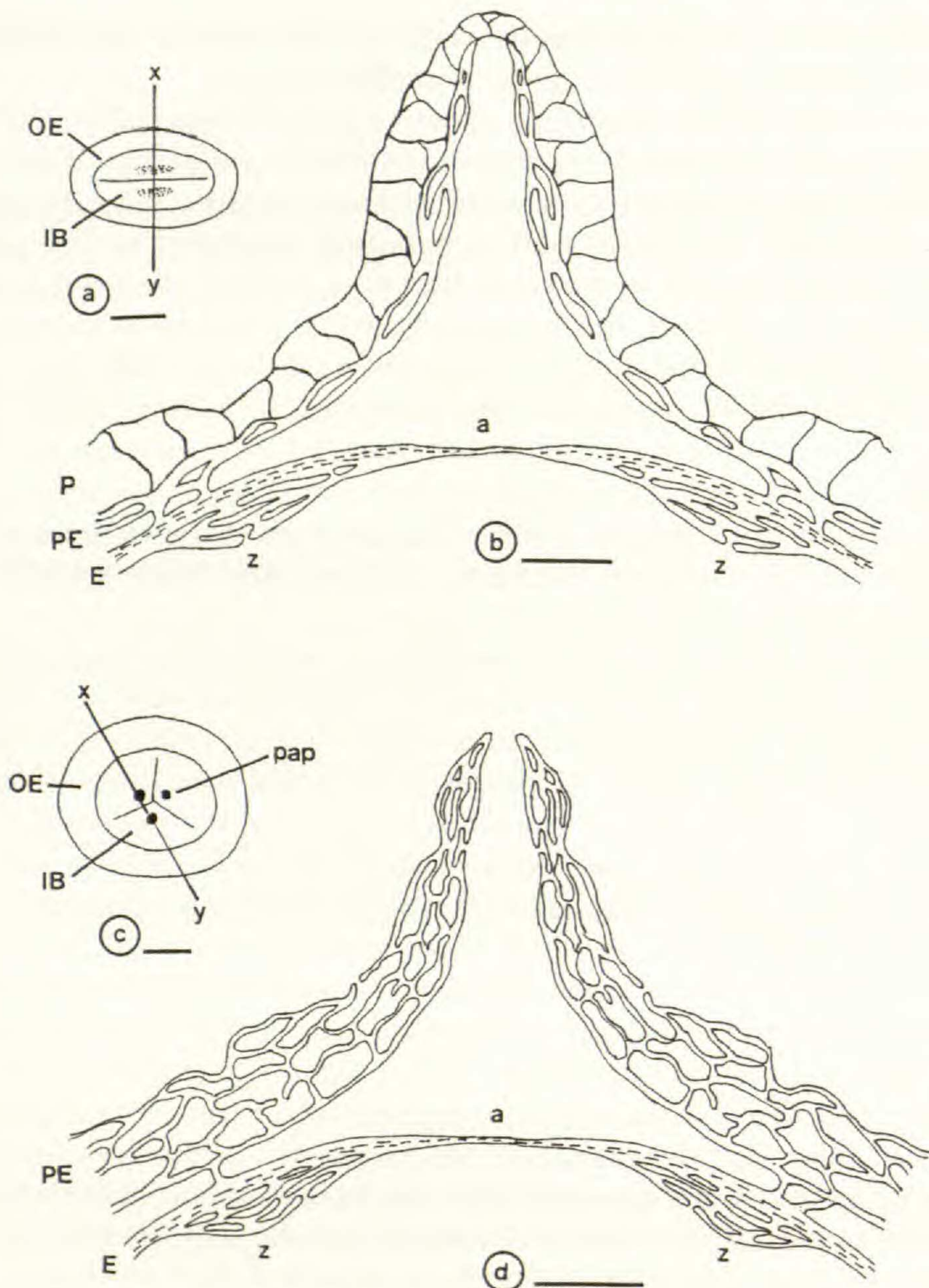
FIG. 4. Comparative ultrastructure of the apertural area in the microspores of *Isoetes* and *Pleuromeia* (scale-bar = 10μm in a, c and 2 μm in b, d). a—*Isoetes*—Diagrammatic representation of the microspore proximal face showing the outer envelope (OE) and the inner body (IB). The dotted spots on both sides of the monolete aperture mark the location of the laminated zones observed with TEM, but indiscernible in intact spores observed with light microscope. b—*Isoetes*. Ultrastructural features of the apertural area of a microspore sectionned along x-y, as shown in Fig. 4a. Note that there are three distinct resistant walls: the exospore (E) with the aperture (a) consisting of a thinner, non-folded wall portion, bordered with laminated zones (z); the para-exospore (PE) forming protruding lips above the aperture; the perispore (P) almost regularly thickened and unbroken above the apical para-exospore lips. c—*Pleuromeia*—Diagrammatic representation of the microspore proximal face showing the outer envelope (OE) and the inner body (IB) with three interradial papillae (pap) arranged between the arms of the trilete aperture and visible with light microscope only in particular conditions of preservation. d—*Pleuromeia*—Ultrastructural features of the microspore apertural area sectionned along x-y, as shown in Fig. 4c. Two distinct walls are preserved: the exospore (E) with the aperture (a) and laminated zones (z) similar to those in *Isoetes*; the para-exospore (PE) which is thicker but structurally analogous with that of *Isoetes* microspores.

the outer envelope, three rounded papillae arranged between the rays of the trilete mark near the proximal pole (Fig. 4c). Ultrastructural investigations in *Pleuromeia rossica* (Lugardon et al., 1997, 1999) and *P. sternbergii* (Grauvogel-Stamm and Lugardon, in prep.) proved that the inner body is a two-layered exospore, uniformly solid and thick except in the proximal region where it shows two notable characteristics (Fig. 4d). In the aperture area indeed, the exospore simply appears thinner without other noticeable differentiation, as in *Isoetes*. Secondly, in each of the three areas lying between the aperture rays, the exospore shows a well-defined laminated zone which is quite similar to those of *Isoetes* microspores, and which obviously corresponds to one of the three interradial papillae observed with light microscope. The outer envelope wholly consists of interconnected elements which show the same electron permeability and reactions to chemical reagents as the outer layer of the exospore, and are surely made up of the same sporopollenin. It is attached to the exospore in the peripheral regions of the proximal face. In the other spore regions, this outer envelope is usually separate from the exospore, and forms a well-marked protrusion divided apically into two lips above each of the three aperture rays.

Thus, the ultrastructural features of the exospore are very similar in *Pleuromeia* and *Isoetes* microspores, in spite of the fact that those of *Pleuromeia* are trilete whereas those of *Isoetes* are monolete. Likewise, the main features of the outer envelope of *Pleuromeia* microspores remarkably resemble those of the para-exospore in *Isoetes,* so that both walls obviously appear homologous, and can be equally called para-exospore. Besides the trilete or monolete condition, the only noteworthy differences lie in the lesser development of the para-exospore and the presence of an extra wall, the perispore, in *Isoetes.*

The combination of the exospore and para-exospore features which is quite identical in *Isoetes* and *Pleuromeia* microspores is also that of the dispersed spore genera *Endosporites* and *Aratrisporites* which are respectively produced by *Chaloneria/Polysporia* and *Annalepis* (Lugardon et al. 2000b, Grauvogel-Stamm and Lugardon, in prep.). The three interradial papillae have been clearly shown in *Endosporites* by Brack and Taylor (1972). This combination of features differentiates these microspores from all the other spore types of extant, and probably fossil, pteridophytes. The aperture consisting of a simply thinner, unfolded exospore area appears unique, and contrasts with the well-marked prominent fold showing various outlines and more or less intricate structures that characterizes the aperture of most pteridophyte spores, including the microspores of Selaginellaceae (Lugardon, 1972, 1980, 1986; Tryon and Lugardon, 1991). Moreover, although the laminated zones are present in the microspores of many Selaginellaceae, they are totally missing in a rather important number of species of this large family (Tryon and Lugardon, 1991: Figs. 231.21, 25, 26,28). Likewise, the para-exospore appears to exist only in very few species of Selaginellaceae in most of which the exospore is devoid of laminated zones, and the para-exospore is almost solid and does not form a sharp protrusion above the aperture (Tryon and Lugardon, 1991: Figs. 231. 26, 28). Among the recent and fossil lycopsids in which the spore ultrastructure

is known to date, the microspores which most resemble those of *Pleuromeia* and *Isoetes* are those of the present *Selaginella selaginoides* (Lugardon, 1972) and those from the Pennsylvanian lycophyte cone *Selaginellites crassicinctus* (Taylor and Taylor, 1990). In both, indeed, the microspores have an exospore with laminated zones and a fairly spongy para-exospore forming prominent lips above the aperture rays. However, these spores are unambiguously distinguishable by the specially narrow, strongly marked apertural fold of the exospore (known only in Selaginellaceae microspores among recent pteridophyte spores, as it can be seen in Tryon and Lugardon, 1991). Thus, not only the microspores of *Isoetes* and *Pleuromeia,* as well as those of *Annalepis* (*Aratrisporites*) and *Chaloneria/Polysporia* (*Endosporites*), show very close ultrastructural similarities, but also they differ markedly from the spores of all the other pteridophyte groups, including the especially variously structured microspores of Selaginellaceae.

It is regrettable that there are no adequate data on the fine features of the microspores of other fossil rhizomorphic lycopsids, particularly the lepidodendrids, which could be compared to those of *Pleuromeia.* The different TEM studies on the lepidodendrid microspores *Lycospora,* achieved by Thomas (1988), Taylor (1990), Hemsley and Scott (1991), Scott and Hemsley (1993), suggest that these microspores also have a thin exospore partly separated from a thicker outer envelope presumably equivalent to a para-exospore. However the *Lycospora* studied by these authors, like those presently investigated (unpublished observations, B.L.), are rather poorly preserved and have not clearly shown the ultrastructural characteristics of their apertural area which, very likely, would provide significant information on the relationships of the lepidodendrids with the other lycopsid lineages.

The megaspores of *Pleuromeia* are also trilete with a slight ornamentation and a spongy aspect rather comparable to that of the microspores (Zhelezkova, 1985; Marcinkiewicz and Zhelezkova, 1992). Ultrastructurally (Lugardon et al., 2000a; Grauvogel-Stamm and Lugardon, in prep.), their exospore consits of a very thin, solid inner layer and a thick spongy outer layer which constitutes most of the wall and is usually divided by a tangential gap in its innermost area, except near the aperture. These features, as well as those of the aperture, are comparable to those of the *Isoetes* megaspores (Lugardon, 1986; Taylor, 1993 ; Tryon and Lugardon, 1991). However they are also analogous to those of all the other, recent or fossil, lycopsid megaspores, so that they do not provide any special phylogenetic information. Nevertheless, the ultrastructural study of especially well-preserved megaspores of *P. rossica* (Lugardon et al., 2000a) demonstrates that the spongy outer layer consists of elements which usually show a rod-like shape, are mostly arranged parallel to the wall surface and are rather widely spaced in moderately crushed spores. These features of the exospore outer layer, which are quite obvious and unvarying throughout the wall in those *P. rossica* megaspores, precisely represent the few characteristics regarded as distinctive of the isoetalean megaspores (Kovach, 1994). Thus the megaspores indicate also, although in a less demonstrative way than

the microspores, the relation joining the Triassic *Pleuromeia* to the living *Isoetes*.

Furthermore, the exospore inner layer of *Pleuromeia* megaspores includes, along both sides of the three apertural arms, a number of laminated zones which are structurally quite similar to those of the microspores. Such laminated zones, that have not been observed in *Isoetes* megaspores, undoubtedly correspond to the "papillae, pustules, cushions, nipple-like projections. . ." described in several morphological studies of fossil lycopsid megaspores. In particular, rather abundant papillae, i.e. 15–20 on either side of each apertural ray, can be observed with LM in the megaspores of *P. sternbergii* (Grauvogel-Stamm and Lugardon, in prep.). However, for the moment these structures do not provide any reliable information on the affinities of *Pleuromeia* since their distribution among the lycopsids is not clearly characterized.

The Triassic lycopsid *Annalepis* and related taxa: comparative study.

Besides *Pleuromeia*, there is another noteworthy Triassic lycopsid, *Annalepis* Fliche, which has long been misunderstood. The type-species, *A. zeilleri* Fliche from the Middle and Upper Triassic of eastern France, is represented by isolated "scales" described by Fliche (1910) who noticed their resemblance to seed scales of the conifer *Araucaria* but finally placed them as an incertae sedis. Grauvogel-Stamm and Duringer (1983) showed that the scales of *A. zeilleri* are sporophylls belonging to the lycopsids and containing microspores assignable to *Aratrisporites*. Such sporophylls are often termed "scales" in descriptions, likely on the basis of their shape and maybe on the analogy of the wording used in the conifer seed scales. Undescribed new material from the Ladinian (late Middle Triassic) of Germany now allows to give some further details, particularly about the rest of the plant (Grauvogel-Stamm and Lugardon, in preparation).

Growth habit and reproductive organs of *Annalepis zeilleri* Fliche.—The sporophylls of *A. zeilleri* are preserved as compressions having 2.5–5 cm long and being slightly trapezoidal in shape (Fig. 5a, 6a). They consist of a long and wide proximal portion flaring abruptly at the base which is somewhat thickened, widening distally and extending by a thick and short, roughly triangular distal portion ending with a small pointed tip. The presence of a transverse wide groove followed by a bulge, distal to the sporangium, between the proximal and distal portions in the sporophylls in compression and adaxial view, indicates that their junction was more or less at right-angle. Indeed, the groove corresponds to the zone of juncture of the two portions and represents exactly the place where the distal portion was straightened up (Fig. 5d-e). This right-angled juncture remained partly preserved and appears as a groove because of the thickness of this zone while the thinner distal portion has been folded back by the sediment pressure and appears in the same plane as the proximal portion in the fossilized sporophylls. Sometimes the groove+bulge appears as a transversal fold (Fig. 5f). Thus, when the sporophylls were packed
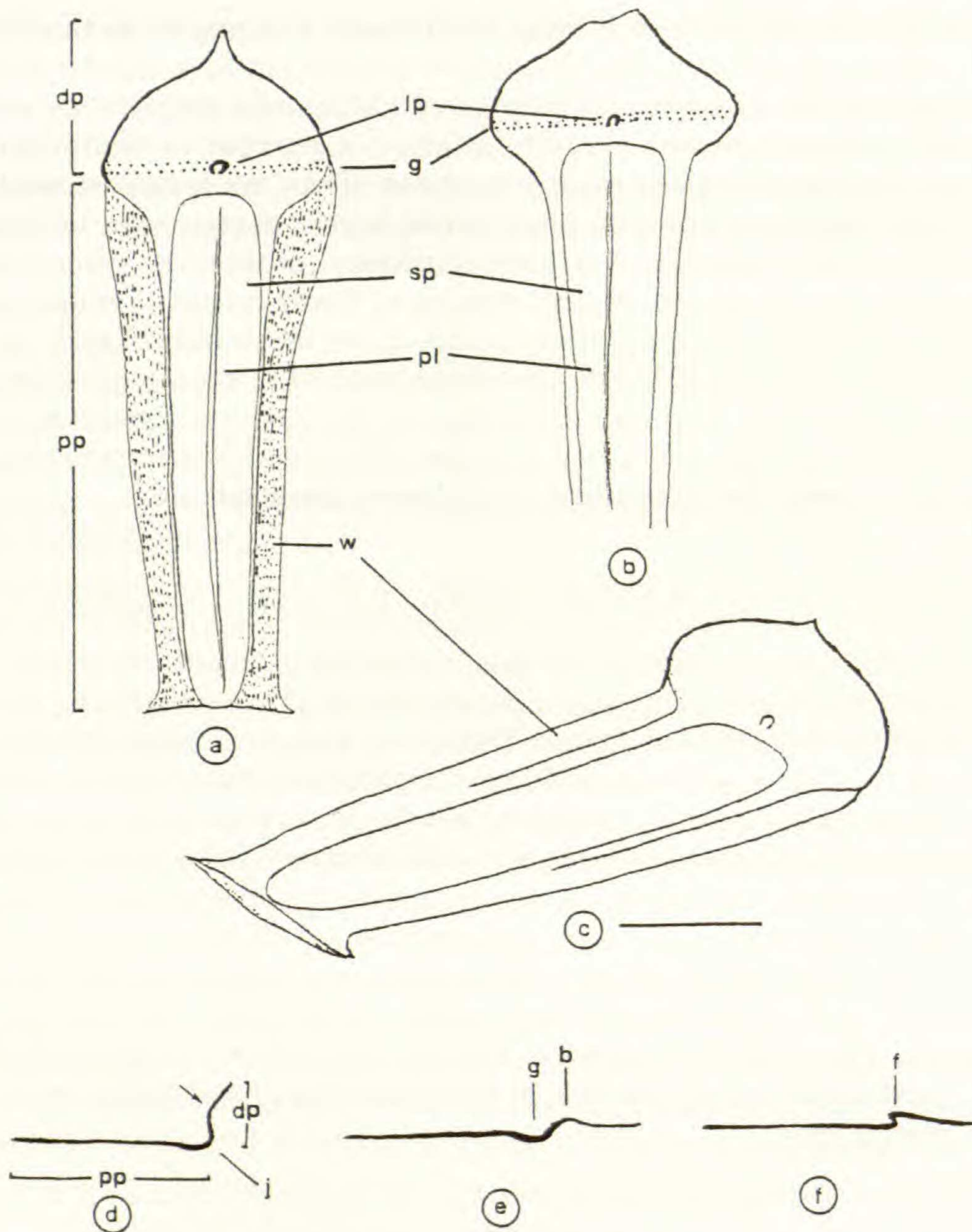
FIG. 5. The sporophyll of *Annalepis zeilleri* Fliche in adaxial view (a-c): (a) in compression, entire; (b) in compression but lacking the lateral wings; (c) in life condition (modified from Grau-vogel-Stamm and Duringer, 1983) (scale-bar = 1 cm). Additional diagrammatic representations of sporophylls in side view (d-f), illustrating how the tranverse groove and either bulge or fold were formed in the junction zone between the proximal and distal portions of the sporophyll during the course of fossilization: (d) sporophyll in life condition, with both portions roughly perpendicular to each other (the arrow indicates the direction of flattening during fossilization); (e) flattened sporophyll with a bulge distal to the transverse groove; (f) flattened sporophyll showing a small fold above the groove. (pp = proximal portion; dp = distal portion, upturned in life position as in c and d; g = transverse groove; b = transverse bulge; f = transverse fold; j = thickened junction zone; sp = sporangium; w = wing; lp = ligular pit; pl = rod-like placenta, located on the abaxial side but often visible on the adaxial side of the sporophylls in compression, especially when the sporangium is empty.
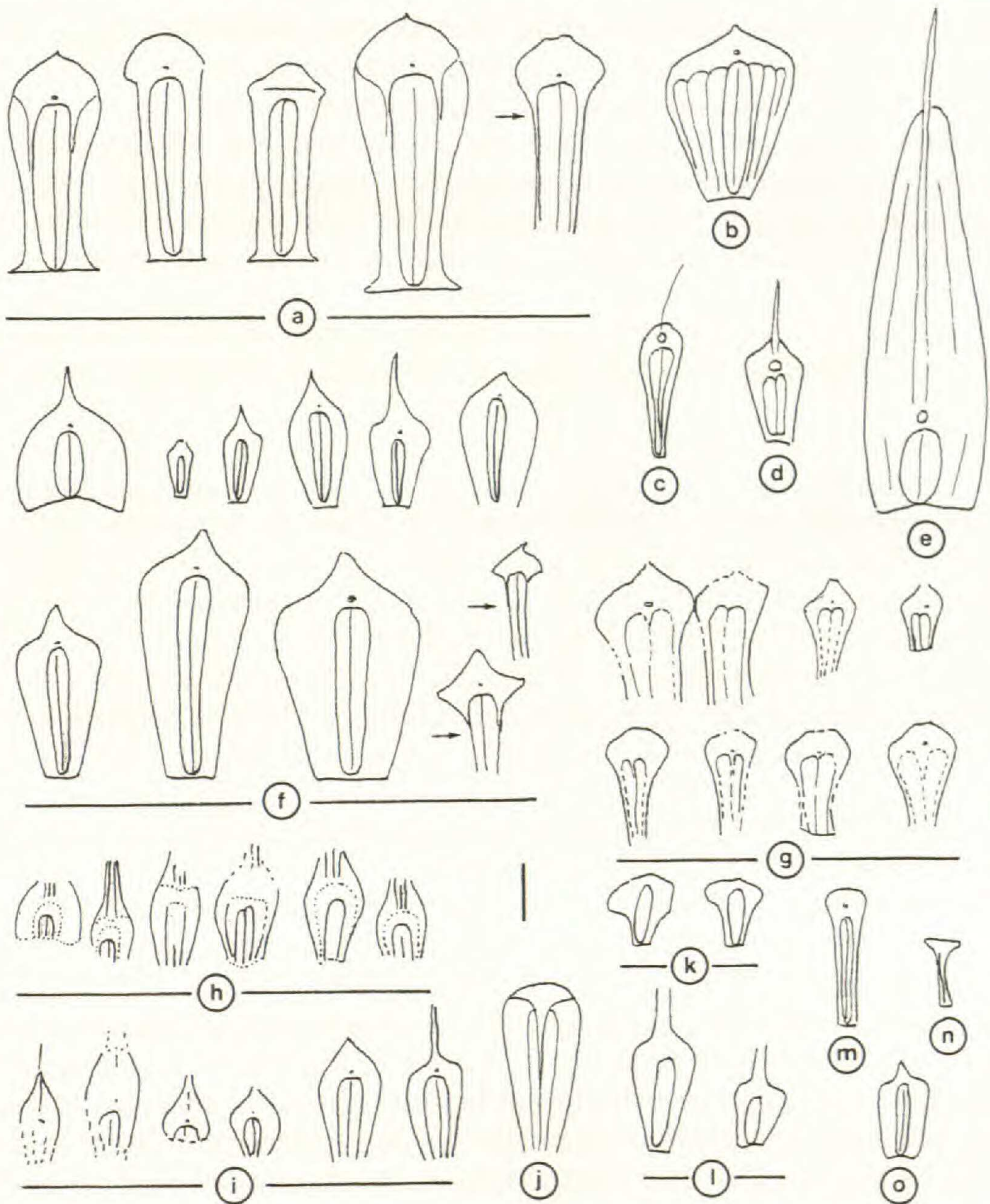
FIG. 6. Comparative morphology of the sporophylls of the *Annalepis*-type and related genera. (Scale-bar = 1 cm). a—*Annalepis zeilleri* Fliche (from Grauvogel-Stamm and Duringer, 1983). The arrow shows a scale having lost its lateral wings. b—*A. latiloba* Meng (redrawn from Meng, 1998). c—*A. angusta* Meng (redrawn from Meng, 1995). d—*A. sangzhiensis* Meng (redrawn from Meng, 1995). e—*A. brevicystis* Meng (redrawn from Meng, 1998). f—*Annalepis* sp. (unpublished). Note the range of variation in shape, size and apex length. The arrows indicate two scales having lost their lateral wings. g—*Isoetes ermayinensis* Wang (redrawn from Wang, 1991). h—*Tomiostrobus radiatus* Neuburg (redrawn from Dobruskina, 1985). i—*Tomiostrobus belozerovii, T. fusiformis, T. bulbosus, T. convexus, T. gorskyi* and *T. migayi*, from left to right (redrawn from Sadovnikov, 1982). j—*Lepacyclotes ellipticus* Emmons (redrawn from Fontaine, 1900). k—*Cylostrobus sydneyensis* Helby and Martin (redrawn from Helby and Martin, 1965). l—*Skilliostrobus australis* Ash (redrawn from Ash 1979). m—*Isoetites daharensis* Barale (redrawn from Barale, 1999). n—*Isoetites horridus* Brown from the Tertiary of North America (redrawn from Hickey, 1977). o—*Isoetites choffatii* (Saporta) (redrawn from Teixeira, 1948) .

together in the cones, their proximal portion was perpendicular to the cone axis whereas their distal part was upturned and more or less parallel to this axis (Fig. 5c). The adaxial surface of the proximal portion was occupied, in the middle and on the whole length, by a long, oval and well-delimited sporangium. The borders of the proximal portion which project on both sides of the sporangium appear to be membranous, as also noticed by Fliche (1910). The boundary between the median part bearing the sporangium and its membranous borders is not always very clear but it is particularly obvious when the imprints are covered with coaly organic matter which is thinner on the borders and therefore less dark than on the other parts of the scales. These membranous borders, called wings or alae according to the authors, likely tended to fall or to be damaged. In some specimens they are partly detached and in others they are completely missing (Fig. 5b), so that it appears clearly that the proximal part is widened distally and that the wings are restricted to the area below this distal widening (see Grauvogel-Stamm and Duringer, 1983; compare figs. 2 and 3 of Pl. 4). The long oval sporangium seems divided by a longitudinal midline which likely corresponds, as in *Isoetes* (Hall, 1971), to the trace of a rod-like placenta which was located on the abaxial side of the proximal portion of the sporophyll and to which the sporangium wall was attached. The presence of a ligule, which was not recognized when Grauvogel-Stamm and Duringer (1983) described these scales, is clear but this ligule is usually decayed and represented only by its attachment point, which is located immediately distal to the sporangium.

Undescribed new material from the Ladinian (late Middle Triassic) of Germany shows that the distal portion of these sporophylls was fleshy. The coalified organic matter covering their imprint is thick and the cell imprints are usually quite visible on its brilliant surface. These sporophylls were arranged in cones reaching at least 8–10 cm in diameter. The occurrence, together with these scales and cones, of several rounded furrowed rhizomorphs, probably 4-lobed, each still attached to a stem (10 cm long preserved) which is covered with oval leaf-scars (the leaves are unknown) is informative since it shows that this plant had the same growth habit as *Pleuromeia* and consisted of an unbranched monopodial axis with a bilaterally symmetrical rooting base and a large, terminal and compact cone (Fig. 7a). The impressive and numerous roots, 3–7 mm wide and more than 30 cm long, which are still attached to the rhizomorphs, may indicate that this plant was robust and strongly anchored. As shown by Grauvogel-Stamm and Duringer (1983), the sporophylls of the cones were monosporangiate, containing either monolete microspores (*Aratrisporites* Leschik) or trilete megaspores (*Tenellisporites marcinkiewiczae* Reinhardt and Fricke). No specimens offer evidence as to whether the cones were bisporangiate or monosporangiate. The ultrastructural features of the monolete microspores are comparable to those of *Pleuromeia* and *Isoetes* (Grauvogel-Stamm and Lugardon, in preparation).

THE OTHER *ANNALEPIS* SPECIES.—Five further species of *Annalepis* have been described from the Anisian (early Middle Triassic) of South China: *A. furo-*
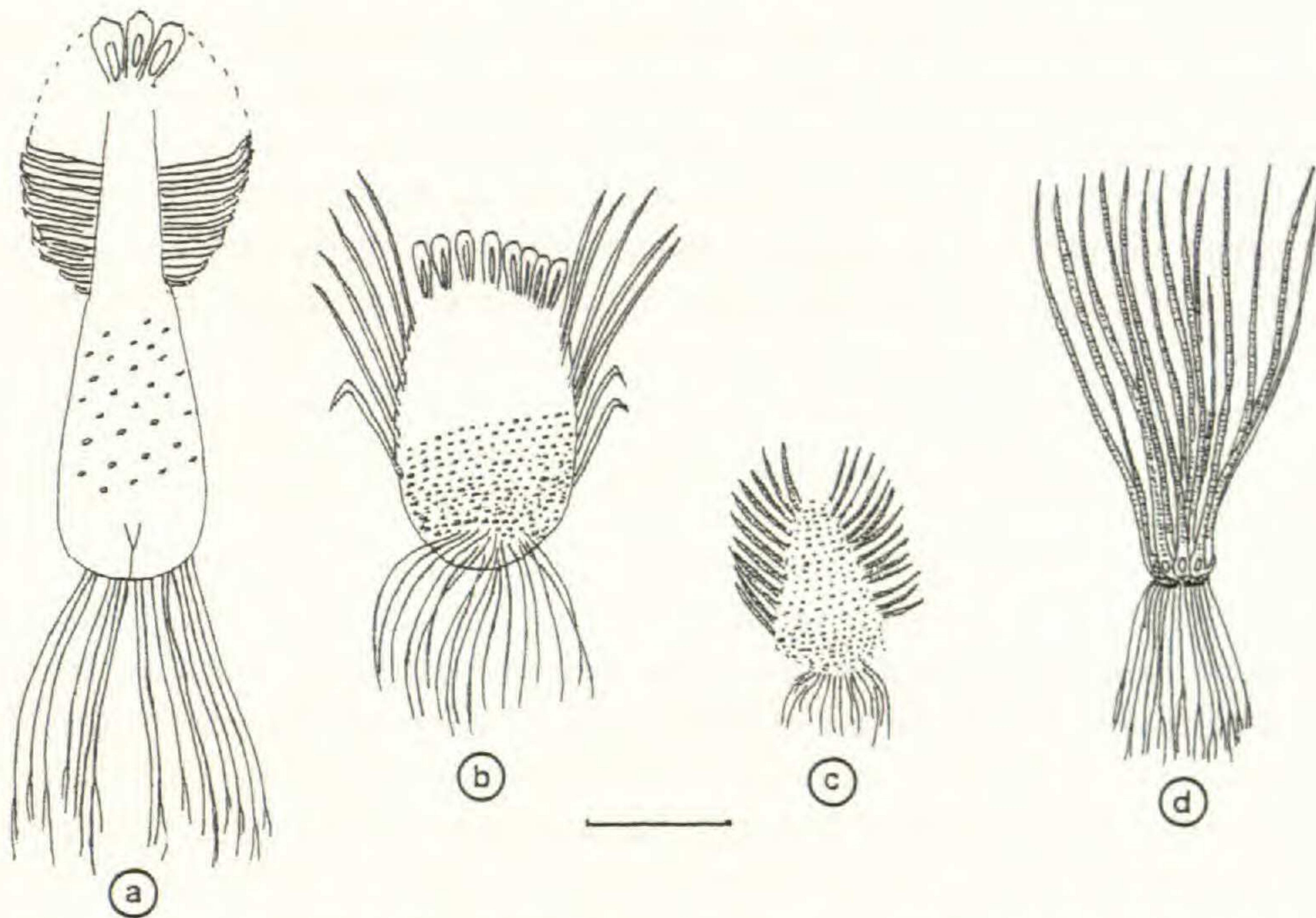
FIG. 7. Comparative growth habit of *Annalepis, Isoetites* and *Isoetes*. (Scale-bar = 5 cm). a—
Annalepis zeilleri Fliche. Note the apical massive cone and the basal rounded rhizomorph bearing
numerous long roots, more than 30 cm long, arranged in two sets on both sides of the furrow. The
leaves are unknown but their scars cover helically the stem. Ladinian of Germany (unpublished).
b—*Isoetites daharensis* Barale. Note the basal rounded rhizomorph and the stocky stem covered
with helically arranged elongated sterile leaves and distal *Annalepis*-type sporophylls which like-
ly were packed in a cone as suggested by the specimens figured by Barale, which are at the origin
of this modified reconstruction. Lower Cretaceous of Tunisia. (modified from Barale, 1999). c—
Isoetites phyllophila Skog et al., showing a conical, elongate corm covered with numerous heli-
cally arranged lacunate sterile leaves. Mid-Cretaceous from North America. (redrawn from Skog
et al., 1992). d—*Isoetes boryana*, having 20–30 lacunate leaves 10–20 cm long (redrawn from
Motelay and Vendryès, 1882)

ngqiaoensis Meng, *A. latiloba* Meng (Fig. 6b), *A. angusta* Meng (Fig. 6c), *A.
sangzhiensis* Meng (Fig. 6d) and *A. brevicystis* Meng (Fig. 6e). The last three
species are shown to have a long, narrow leaf tip emerging abruptly from a
rounded apex (Meng, 1995, 1996, 1998, 2000). The sporophylls representing
A. brevicystis are by far bigger than the others and greatly differ in shape. Meng
(1998) moreover described several further sporophylls with a long leaf tip con-
taining transverse partitions which he assigned to *A. zeilleri* but which prob-
ably correspond to another species. Indeed none of the specimens correspond-
ing to the original material of *A. zeilleri* described from the Ladinian (late
Middle Triassic) of France show such features (Grauvogel-Stamm and Durin-
ger, 1983). In all the sporophylls described by Meng, the sporangium is tongue-
shaped and is longitudinally divided by a midline. Unfortunately none of the
photographic illustrations of the Chinese specimens clearly shows the struc-
ture of these sporophylls, such as it is shown in the rough reconstructions
figured by Meng (1995, 1998, 2000).

Furthermore, an assemblage of numerous undescribed sporophylls from the
Ladinian (late Middle Triassic) of Germany which is here provisionally as-

signed to *Annalepis* sp. (Fig. 6f), represents a further new species which is still under study (Grauvogel-Stamm and Kelber, in preparation). Indeed, these sporophylls which originally have been attributed to *A. zeilleri* by Kelber and Hansch (1995) contain features which distinguish them from this species. They show a great variability in shape, size and apex length, which probably depends on their place within the cone. Transverse partitions have never been observed in any of the long apex of these sporophylls. However, they seem to have lateral membranous borders as in *A. zeilleri* (Fig. 8a,b) and the tongue-shaped sporangium shows a longitudinal midline as in the other *Annalepis*-like sporophylls.

In spite of a roughly similar organization, the sporophylls of *Pleuromeia* and *Annalepis* differ in several respects. Their general outline and the shape of their sporangium are quite different. The wings bordering the sporophyll proximal part and the longitudinal midline running along the sporangium in *Annalepis* are missing in *Pleuromeia*. In contrast to the sporophylls of *Annalepis* that are clearly differentiated into a proximal and a distal portions which were very likely more or less perpendicular to each other in lifetime, those of *Pleuromeia* do not show such a morphological partition and are approximately on the same plane from the base to the apex. Moreover, in *Pleuromeia* the microspores and megaspores are trilete whereas in *Annalepis* only the megaspores are trilete while the microspores are monolete (Grauvogel-Stamm and Duringer, 1983), as those of Isoetes.

THE ALLIED GENERA: FROM *ANNALEPIS* TO *ISOETITES*.—While it is easy to recognize a sporophyll as belonging to the genus *Pleuromeia*, there are difficulties in identifying those of the *Annalepis*-type. Most of the latter have been long misunderstood, being first regarded as araucarian seed scales and therefore often assigned to the genera *Araucarites* Presl or *Pseudoaraucarites* Vladimirovitch (Dobruskina, 1985). Now, eventhough they are regarded as lycopsids, these sporophylls are assigned to different genera as *Tomiostrobus* Neuburg, *Skilliostrobus* Ash, *Cylostrobus* Helby and Martin and *Lepacyclotes* Emmons, and classified, together with *Annalepis,* as satellite-taxa in the Pleuromeiaceae (Thomas and Brack-Hanes, 1984). However their taxonomic position is greatly in flux. Dobruskina (1985) stressed the similarity between *Annalepis* and *Tomiostrobus* whereas Retallack (1997) synonymized *Annalepis* with *Lepacyclotes*. Moreover Sadovnikov (1982) and Retallack (1997) synonymized *Skilliostrobus* with *Tomiostrobus*. Nevertheless, since the genus *Annalepis*, particularly the type-species *A. zeilleri,* is the best known, it is here regarded as the type of this kind of sporophyll. *Lepacyclotes* was described earlier by Emmons (1856) but the precise structure and the in situ spores have never been studied. Other taxa for which the structure and the shape of the sporophylls are unknown include *Lycostrobus scotti* Nathorst and *Austrostrobus ornatum* Morbelli and Petriella. As for *Lycostrobus chinleana* Daugherty from the Triassic of southwestern USA, it has proven to be an equisetalean reproductive organ (Grauvogel-Stamm and Ash, 1999) and not a lycopsid, as previously believed, or an arborescent quillwort, as recently asserted by Retallack (1997).
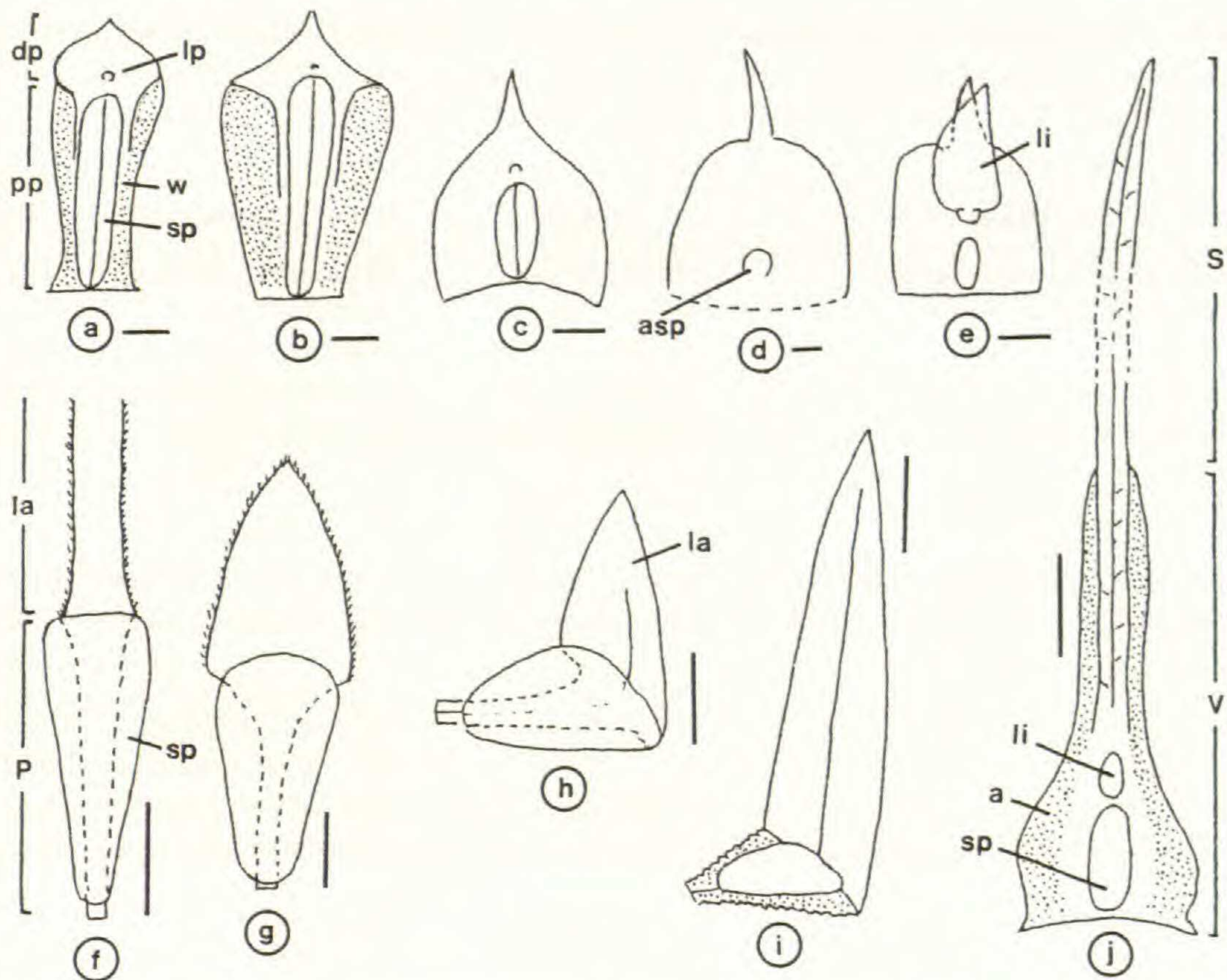
FIG. 8. Comparative morphology and terminology of the sporophylls of *Annalepis*, Lepidodendrids and *Isoetes* in adaxial views. (scale-bar = 5mm, except in d,e = 1mm). a—*Annalepis zeilleri* Fliche (pp, proximal portion; dp, distal portion; lp, ligular pit; sp, sporangium; w, wing). Note the clearly delimited wings (stippled) of the proximal portion (modified from Grauvogel-Stamm and Duringer, 1983). b, c—*Annalepis* sp. (undescribed): two sporophylls within the range of variation. The wings (stippled) are clearly delimited in b, while they are not in c. d—*Isoetes coromandelina* Lin. Fils: a scale-leaf with an aborted sporangium (asp) (redrawn from Srivastava and Wagai, 1996, Pl.4 Fig. 1). e—*Isoetes* sp.: a leaf primordium with the developing ligule (li) and sporangium (redrawn from Kubitzki and Borchert, 1964). f—*Cyclostigma kiltorkense* Haughton (p, pedicel; la, lamina; sp, sporangium). Note the narrow pedicel slightly widened distally below the sporangium and the distal lamina that is linear lanceolate, up to 8 cm long (modified from Chaloner, 1968). g—*Lepidostrobus bohdarowiczii* Bochenski. The narrow pedicel is here markedly widened distally (modified from Bochenski, 1936). h—*Lepidostrobus jenneyi* (White) Abbott. Sporophyll showing a proximal pedicel below the sporangium and an apically directed lamina (la). Due to its strong distal widening, the pedicel has been described T-shaped by Abbott (modified from Abbott, 1963). i—*Lepidocarpopsis lanceolatus* (Lindley and Hutton) Abbott. The pedicel clearly bears well-developed wings (stippled) and therefore exceeds the width of the sporangium (modified from Abbott, 1963). j—*Isoetes triquetra* A. Braun. Sporophyll showing the vagina (v) with lateral alae (a, stippled), sporangium (sp), ligula (li), and the terminal subula (s) 3,4 cm long (modified from Kubitzki and Borchert, 1964; terminology after Hickey 1985).

Since the precise structure and shape of the sporophylls are essential for identifying and comparing these lycopsids, only the genera for which these features are known with considerable accuracy and which resemble the *Annalepis*-type sporophylls are listed in Table 1 and shown in Fig. 6, Some *Isoetites* are also listed but their inclusion raises some questions on the exact interpretation of this fossil genus, as commented below.

TABLE 1. The *Annalipis*-like sporophylls. Data taken from the following sources: [1]Fliche (1910); [2]Meng (1995); [3]Meng (1998); [4]Meng (2000); [5]Dobruskina (1985); [6]Sadovnikov (1982); [7]Wang (1991); [8]Emmons (1856); [9]Ash (1979); [10]Helby and Martin (1965); [11]Teixeira (1948); [12]Barale (1999); [13]Brown (1958), Hickey (1977).

Taxon	Age	Occurrence	Figure
Annalepis zeilleri[1] (type-species)	Middle Triassic	NE France; Germany	Fig. 6a
A. furongqiaoensis[4]	Middle Triassic	Southern China	
A. latiloba[3]	Middle Triassic	Southern China	Fig. 6b
A. angusta[2]	Middle Triassic	Southern China	Fig. 6c
A. sangzhiensis[2]	Middle Triassic	Southern China	Fig. 6d
A. brevicystis[2]	Middle Triassic	Southern China	Fig. 6e
Annalepis sp. (undescribed)	Middle Triassic	Germany	Fig. 6f
Isoetes ermayinensis[7]	Middle Triassic	North China	Fig. 6g
Tomiostrobus radiatus[5] (type-species)	Lower Triassic	South Siberia, Russia	Fig. 6h
T. belozerovii[6]	Lower Triassic	East Siberia, Russia	Fig. 6i
T. fusiformis[6]	Lower Triassic	East Siberia, Russia	Fig. 6i
T. bulbosus[6]	Lower Triassic	East Siberia, Russia	Fig. 6i
T. gorskyii[6]	Lower Triassic	East Siberia, Russia	Fig. 6i
T. migayi[6]	Lower Triassic	East Siberia, Russia	Fig. 6i
T. convexus[6]	Lower Triassic	East Siberia, Russia	Fig. 6i
Lepacyclotes circularis[8] (type-species), syn. *L. ellipticus*[8]	Upper Triassic	North Carolina, USA	Fig. 6j
Cylostrobus sydneyensis[10] (type-species)	Lower Triassic	Australia	Fig. 6k
Skilliostrobus australis[9] (type-species)	Lower Triassic	Australia	Fig. 6l
Isoetites daharensis[12]	Lower Cretaceous	Southern Tunisia	Fig. 6m
Isoetites horridus[13]	Tertiary	North America	Fig. 6n
Isoetites choffati[11]	Lower Cretaceous	Portugal	Fig. 6o

The sporophylls characterizing these taxa share a remarkable similarity with *Annalepis*. They have a comparable shape and structure (Fig. 6a-o). Most of them (*Annalepis, Tomiostrobus, Isoetes ermayinensis, Skilliostrobus, Cylostrobus*) contain microspores assignable to *Aratrisporites* (Balme, 1995). In all, the sporangium is elongate-oval and shows a longitudinal midline which has been variously interpreted. In *Annalepis zeilleri*, Grauvogel-Stamm and Duringer (1983) suggested that it might represent the trace of the vascular bundle (Fig. 6a). In *Isoetites daharensis* (Fig. 6m), this line, which is obvious too and quite resembles that of *Annalepis*, has been interpreted as being the internal boundary of the velum (Barale, 1999). In *Isoetes ermayinensis* (Fig. 6g) it has been regarded as a strong keel or a vascular bundle (Wang, 1991). In *Tomiostrobus* (Figs.6h,i), Sadovnikov (1982) interpreted it as a keel whereas Dobruskina (1985) regarded it as the vascular bundle. Fontaine (1900) also regarded it as a keel in *Lepacyclotes ellipticus* (Fig. 6j). The fact that this line appears invariably the same in the different scales indicates that it is a characteristic feature of this kind of sporophyll and that it has the same significance in all. A comparison with *Isoetes* shows that it does not represent the velum which is a thin membrane covering partially or entirely the sporangium and which never has a longitudinal slit-like free edge in the middle. In contrast, the longitudinal midline more likely indicates that, as in *Isoetes* (Hall, 1971), a rod-

like placenta including the vascular bundle existed on the abaxial side of these sporophylls, to which the sporangium wall was attached, and that it became apparent on the adaxial side of the compressions particularly when the sporangium was empty. According to J. Hickey (pers. com), in *Isoetes* this placenta is represented by a pad of vascularized tissue which often intrudes into the sporangium and runs lengthwise. Hall (1971) moreover noticed that in dried specimens of *I. tenuifolia* and *I. pitotii,* the rod-like shaped placenta shrinks and leaves an especially deep and profound groove.

In some specimens of *Tomiostrobus* (Figs. 6h,i) and *Skilliostrobus* (Fig. 6l) which one of us (L. G.-S.) observed, and according to the illustrations of *Isoetes ermayinensis* (Fig. 6g) and *Cylostrobus sydneyensis* (Fig. 6k), most of the scales seem to have a proximal portion with lateral wings, as in *A. zeilleri* (Fig. 6a). These lateral wings are clearly shown in the transverse section of the sporophyll of *Tomiostrobus* figured by Sadovnikov (1982, Fig. 2, at right), though not noticed by him. They are comparable to those shown in transverse sections of *Isoetes* sporophylls (Pitot, 1959; Hall, 1971). In some specimens the wings seem to be missing or partly destroyed, as in *Skilliostrobus* (see Ash, 1979, Figs. 7 A–D) or *I. ermayinensis* (see Wang, 1991, Pl. 1 figs. 9–11, 13, 14). However the question of the wings would require further investigations since their presence has not been noticed in most of the sporophylls listed in Table 1.

The long, oval and contiguous depressions, often visible on both sides of the sporangium in most of the scales, such as *Annalepis* sp., *A. zeilleri,* *A. latiloba* and *Lepacyclotes circularis,* correspond to the imprint of the sporangia of the underlying and overlying sporophylls when they were packed together in the cone.

The wide transverse groove visible at the junction of the proximal and distal, thick portions of the scales of *L. circularis,* as seen in adaxial view and as figured by Bock (1969, Figs. 93–94), is quite similar to that observed in *A. zeilleri* (Grauvogel-Stamm and Duringer, 1983, Pl. 4 figs. 2,3); this strongly suggests that the proximal and distal portions were originally more or less perpendicular to each other in *Lepacyclotes* too. The sporophylls of *Tomiostrobus* which one of us (L.G.-S.) observed, also show that the junction of the proximal and distal portions was more or less right-angled. Likewise, in *Annalepis* sp., the distal portion also seems to have been upturned. Also Meng (1998) noticed the presence of a transverse ridge in *A. latiloba* which suggests that the sporophyll distal portion was more or less perpendicular to the proximal one.

However various interpretations and/or misinterpretations have occurred because these sporophylls often have a more or less blunt, seemingly incomplete apex and/or because the scale tip has been considered as being the ligule, making the interpretation of this area confusing. Moreover, some of these sporophylls have been regarded as having lost their leafy distal portion. The sporophylls of *Isoetes ermayinensis* Wang (Fig. 6g) are so similar to those of *A. zeilleri* (Fig. 6a) that the inclusion of that taxon in *Isoetes* is surprising. In fact, Wang (1991) interpreted the numerous, associated elongate leaf imprints as their detached apical parts. These imprints contain transverse partitions that

he supposed to be collapsed air chambers, similar to those of *Isoetes*. However no specimens show them in organic connection. A similar leaf imprint found associated with sporophylls of *A. brevicystis* in the Anisian of South China has also been regarded as their tip (Meng, 1996, Pl. 2 Fig. 14). Sterile partitioned leaves have never been found associated with *A. zeilleri* from the Triassic of eastern France (Grauvogel-Stamm and Duringer, 1983). Retallack (1997) noticed that Wang's sporophylls of *I. ermayinensis* are "unlikely to have borne the wider undulose leaf fragments on their tips as in *Isoetes*" and reassigned *I. ermayinensis* to the genus *Lepacyclotes*. Likewise, the reassignment of *Lepacyclotes circularis* and *L. ellipticus* to the genus *Isoetites*, as proposed by Brown (1958), does not seem to be justified and has been questioned by Chaloner (1967) and Bock (1969) since these scales have a short and well delimited triangular apex and are devoid of any traces of a long sterile leafy portion comparable to that of *Isoetes*. Skog and Hill (1992) also questioned this reassignment and noticed the resemblance between *Lepacyclotes circularis* and *Annalepis*. Among the fossils attributed to the genus *Isoetites*, there are also isolated scales with a small pointed apical tip resembling the scales of *Annalepis*, which have been supposed to be the fertile base of *Isoetes* leaves. It is the case, especially, of *Isoetites horridus* (Fig. 6n) from the Tertiary of North America (Brown 1958, Figs. 1,3; 1962, Pl. 9 Fig. 1) and *I. choffati* Saporta (Fig. 6o) from the Cretaceous of Portugal (Teixeira, 1948, Pl. XXVI figs. 7–8). However the small apical tip is not preserved in some specimens, as those of *I. horridus* from the early Tertiary of Dakota figured by Hickey (1977, Pl. 1 figs. 6,7) and described as being dumb-bell shaped by Collinson (1991). Moreover, according to the illustration of Collinson (1991, Fig. 7.3h), which shows a circlet of such supposed fertile leaf bases, one can see that Hickey (1977) represented these sporophylls upside down and that the narrower extremity corresponds to the base while the broader one corresponds to the distal extremity to which the long leafy part was supposed to be attached. It is noteworthy that this circlet closely resembles those consisting of *Annalepis* sporophylls. Since the leaf tip is often missing in the *Isoetites* remains, Collinson (1991) suggested that this tip was deciduous in the fossil genus. In *Isoetes*, the long leafy part is usually not deciduous, except in some terrestrial species where the distal portion of the leaves erodes away leaving only a leaf base, typically with a sporangium (J. Hickey, pers. com.).

However, the fossils attributed to *Isoetites* call for several remarks. An overview of these fossils shows that the precise shape and structure of the fertile parts are usually poorly described and illustrated and that their relationship with the sterile leaves is not clear. For most taxa, the fertile and sterile parts are not shown in organic connection and several rhizomorphs and stems seem to contain only sterile leaves, e.g., *Isoetites phyllophila* (Skog et al., 1992), *I. horridus* (Brown, 1962; Hickey, 1977), *I. indicus* (Bose and Banerji, 1984), *I. serratus* (Brown, 1939), *I. rolandii* (Ash and Pigg, 1991) and *Cylomeia* (White, 1981) which is now reassigned to *Isoetes beestonii* (Retallack, 1997). It is surprising that none of them shows any trace of a sporangium at the base of the leaves. Likewise, the late Cretaceous and Tertiary specimens assigned to *Is-*

oetites by Pigg (2001) do not show clearly if there were sporangia at the base of the leaves. Long sterile leaves, without partitions, still attached to an axis have also been found associated with the sporophylls of *Annalepis* sp. in the Triassic of Germany and have been assigned to *Isoetites* sp. (Kelber and Hansch, 1995). In *Isoetes*, a great number of leaves are usually fertile (Jermy, 1990) and when once the plant becomes fertile, all subsequently produced leaves will either be fertile or at least initiate a sporangium (J. Hickey, pers. com.). During the ontogeny of the *Isoetes* leaves, the sporangium develops very early (Fig. 8e), is already discernible in the leaf primordia (Bhambie, 1963; Kubitzki and Borchert, 1964), and even the vegetative leaves have an aborted sporangium at the base (Pitot, 1959; Rauh and Falk, 1959; Kubitzki and Borchert, 1964). Thus the real nature of many *Isoetites* leaves remains quite ambiguous. Moreover, some of the described *Isoetites* species do not represent lycopsids. According to Skog and Hill (1992), *Isoetites gramineus* (Ward) Bock more likely is an osmundaceous fern and *I. bulbosus* Drinnan and Chambers more probably corresponds to "pentoxylalean fertile short shoots".

Likewise, the interpretations about the scales of *Isoetites* having a small tip and resembling the *Annalepis* sporophylls are still questionable. Do they represent fertile leaf bases which have lost their leafy extremity, and is the small tip visible in some of them actually a ligule? In *Isoetes*, the ligule is a delicate ephemeral parenchymatous flap which is mostly deciduous and tends to disappear at maturity (Pitot, 1959; Bhambie, 1963; Goswami, 1976; Kott and Britton, 1985). Therefore, it seems unlikely that the ligule would persist if the long leafy extremity of the sporophyll was destroyed, as for example in *I. horridus* where a specimen representing a circlet of sporophylls still attached to an axis has been interpreted by Brown (1962, Pl. 9 Fig. 1,3) as being a "corm with sporangia tipped by ligules". The *Isoetites* scales with a small apical tip seem more likely to represent entire sporophylls rather than the basal part of fertile leaves, and their small apical tip more likely represents their actual extremity and not the ligule. Moreover, the fact that these *Isoetites* sporophylls with short pointed or blunt apices are often found associated with long, apparently sterile, leaves and are still closely packed (see Brown, 1958 Fig. 3; Hickey, 1977; Collinson, 1991, Fig. 7h; Barale, 1999, Fig. 5)—as in the circlets of sporophylls of *I. horridus, A. zeilleri, Annalepis* sp. and *Lepacyclotes ellipticus* - suggests that they represented distinct organs, occupied a place distinct from that with sterile leaves, and became detached or abcised from an axis. *Isoetites daharensis* (Fig. 7b) is particularly interesting in this respect since it has a rounded rhizomorph with roots and a short stem bearing distal scale-like sporophylls and elongate sterile leaves (Barale, 1999). Such a plant does not conform to *Isoetes* (Fig. 7d) in which the sterile and fertile leaves are morphologically similar (Jermy, 1990) but more closely resembles *Annalepis* or *Pleuromeia* in which the fertile and sterile leaves differ and are located in distinct places on the plant. *Isoetites daharensis* (Fig. 6m) is all the more interesting because its sporophylls are of the *Annalepis*-type, as are those of *I. horridus* (Fig. 6n). However, contrary to the latter, in *I. daharensis* the leaves are not lacunate. In most of these fossil lycopsids, the length of the corm plus stem is unknown.

In *I. daharensis* (Fig. 7b), the rounded corm + stem are 11 cm tall (Barale, 1999) as in *Annalepis zeilleri* (Fig. 7a). In *Isoetites phyllophila* (Fig. 7c), the rhizomorph is elongate, conical, and 6 cm high (Skog et al., 1992). However, as noticed by Skog and Hill (1992), there are no broadly ranging studies on the shape of the stems at various stages in development of extant species of *Isoetes* stripped of their appendages and de-corticated, so it is difficult to compare fossil and living plants. In *Stylites* for example, the stem reaches 20 cm long (Rauh and Falk, 1959). Likewise, there are no broadly ranging studies on the distribution of the fertile and sterile leaves in extant *Isoetes*.

Clearly, most of the *Isoetites* specimens need further investigation and better illustrations, all the more since this genus is regarded as representing primitive *Isoetes* and is included in the subgenus *Euphyllum*, together with three extant species of *Isoetes* (Hickey, 1986, 1990; Taylor and Hickey, 1992).

Nevertheless, this comparative analysis of the sporophylls of *Annalepis* and related taxa (*Tomiostrobus, Lepacyclotes, Skilliostrobus,* some *Isoetites*) demonstrates that all these sporophylls have a similar basal unit which is narrow at the base, widens distally and extends by a short, roughly triangular distal portion ending with a more or less long pointed apical tip. In all there is a long oval adaxial sporangium and a ligule immediately distal to it. In most of them moreover, the proximal portion appears to bear lateral wings which are restricted to the area below the widened portion of the leaf. The sporophyll of *Isoetites horridus* figured by Hickey (1977, Pl. 1 figs. 6,7) is especially interesting in this respect because it shows particularly well the distal widening (Fig. 6n), suggesting that initially it also had lateral wings restricted to the proximal part.

RESEMBLANCES WITH *ISOETES* AND LEPIDODENDRID SPOROPHYLLS.—Besides the ultrastructural similarities of the spores of *Annalepis* and *Isoetes* (Lugardon et al. 2000b; Lugardon and Grauvogel-Stamm, in prep.), there are still some other morphological resemblances between both genera which deserve to be noticed.

Indeed, some *Annalepis* sporophylls (Fig. 8c) closely resemble the developing leaf primordia of *Isoetes* (Fig. 8e), which have a short pointed apex devoid of air chambers and an almost fully developed ligule, proximal to this apex (Kubitzki and Borchert, 1964). Such a resemblance shows how an *Annalepis* sporophyll may have developed into an *Isoetes* sporophyll. It would be instructive to know the shape and growth sequence of the wings in young *Isoetes* leaves but this development has not been studied (J. Hickey, personal information, September 1999).

Likewise it is noteworthy that the *Annalepis* sporophylls much resemble the scale leaves which occur in many *Isoetes* species and differ greatly from the typical *Isoetes* long leafy sporophylls. These scale leaves which are mostly unknown to *Isoetes* non-specialists are present at the growing apex and at the base of the corm, but are also said to occur below the spirally arranged leafy sporophylls, sometimes intermingled with them, and to form two or three whorls in old corms (Duthie, 1929; Stolze and Hickey, 1983; Hickey, 1986; Srivastava and Wagai, 1996). Thus for example, within the range of variation

of *Annalepis* sp. there are sporophylls (Fig. 8c) which are very similar to the scale leaves of *Isoetes montezumae* A.A. Eaton (Stolze and Hickey, 1983, Fig. 10c) or *I. coromandelina* Lin. fils (Srivastava and Wagai, 1996, Pl. 4 Fig. 1) (Fig. 8d). Likewise, the sporangium bearing scales with a small pointed apical tip (Fig. 6o) which occur in *Isoetites choffati* (Teixeira, 1948) among the long leafy *Isoetes*-like sporophylls, and which resemble the sporophylls of *Annalepis*, might also represent such scale leaves. According to Hickey (pers. com.), the scale leaves of *Isoetes* are environmentally induced and occur in distinct zones (alternating with typical fertile leaves) as a result of seasonality. Also according to Hickey (1986), they have a protective function for the corm and represent leaf primordia in which the development has become arrested. However, their resemblance with *Annalepis* sporophylls suggests that they also might have a phylogenetical significance and might represent vestigial remnants of ancestral sporophylls, indicating that the genus *Annalepis* is an ancestor of *Isoetes*.

The sporophylls which have been described recently from the Triassic of South China and which have been assigned to several new *Annalepis* species, e.g. *A. angusta* (Fig. 6c), *A. sangzhiensis* (Fig. 6d), *A.brevicystis* (Fig. 6e) and *A. zeilleri* (sensu Meng 1998) are also particularly interesting in the comparison between *Annalepis* and *Isoetes*. Indeed, these sporophylls which are characterized by a long, narrow (spur-like) outgrowth, arising distal to the ligular pit, running across the short, wide, triangular to rounded distal portion and extending far beyond it, also closely resemble the scale leaves which occur in *Isoetes* and which are characterized by a spine-like apex. In *I. mahadevensis* for instance, the scale apices are said to appear as spur-like outgrowths and to emerge abruptly from an almost rounded region (Srivastava and Wagai, 1996). In *Annalepis zeilleri* (sensu Meng 1998) moreover, this apical outgrowth is described as containing transverse partitions. Meng (1998) interpreted it as the leaf tip of the sporophylls. According to Hickey (pers. com.), it is comparable to the "subula" of the *Isoetes* leaves, i.e. their distal awl-like shaped outgrowth. Meng (1998, 2000) also noticed the similarity of the *Annalepis* sporophylls with *Isoetes* leaves, and suggested that *A. brevicystis*, especially, might be ancestral to the living genus.

The new Chinese *Annalepis* species are moreover particularly interesting because they allow to understand some unexplained features of *Tomiostrobus radiatus* (Fig. 6h). Indeed, the two parallel lines shown to arise distal to the ligule and to extend apparently out from the fragmentary apex of the sporophylls in the rough drawings of Dobruskina (1985, Fig. 1b-e, g, i, n), more likely represent partially preserved apical spine-like outgrowths comparable to those described by Meng (1995, 1998, 2000) in several Chinese *Annalepis* species and compared by Hickey (pers. com.) to the subula of the *Isoetes* leaves. In a sporophyll of *T. radiatus* figured by Yaroshenko (1988, Fig. 11), the long apex appears moreover to contain transverse ridges in the middle, though not noticed by the author, which might represent collapsed air chambers. However, none of the fragmentary sporophylls attributed by Sadovnikov (1982) to several distinct *Tomiostrobus* species (Fig. 6i) seems to contain such

partitions. Likewise, in none of the specimens of *Tomiostrobus* from the Lower Triassic of East and North Siberia (Russia) which one of us (L. G.-S.) could observe, the apex shows such features. Comparable unexplained spur-like outgrowths seem to exist in *Annalepis* sp. and *A. zeilleri* but they are badly preserved and have not yet been described (Grauvogel-Stamm and Lugardon, in preparation; Grauvogel-Stamm and Kelber, in preparation).

However, in spite of these resemblances there are some differences in the shape of the fertile area and lateral wings between the *Annalepis* sporophylls and the typical *Isoetes* long fertile leaves. In *Isoetes* the proximal portion is wide at the base, narrows distally and extends upwards in a long leafy extremity (Fig. 8j), whereas in *Annalepis* and allied genera the proximal portion is narrow at the base, widens distally and extends by a short more or less triangular portion ending in a small pointed apical tip (Fig. 8a, b). In *Annalepis* moreover the lateral wings are restricted to the area below the distal widening whereas in *Isoetes* the winged borders, now commonly termed alae, extend upwards over a variable length (Kott and Britton, 1985). It is worthy of note that in most of the extant *Isoetes* species, these alae are also restricted to the proximal portion of the leaf (Hickey, 1986; Taylor and Hickey, 1992) but, in contrast to *Annalepis,* they are not limited by a distal widening of that proximal portion.

In fact the shape of the proximal part and lateral wings of *Annalepis* sporophylls more resembles that of the basal unit of the sporophylls of the Carboniferous lepidodendrids *Lepidostrobus* Brongniart, *Lepidostrobopsis* Abbott and *Lepidocarpopsis* Abbott, as already noticed by Grauvogel-Stamm and Duringer (1983, Figs. 3a, b). These lepidodendrid sporophylls that have usually a long, wide, upturned leafy distal portion termed lamina in most descriptions, also have a basal unit consisting of a proximal portion bearing an adaxial sporangium and sometimes lateral wings, which is termed pedicel (Fig. 8f-i). It is noteworthy that the proximal portion of these sporophylls widens distally as in *Annalepis* or *Isoetites horridus* (Hickey, 1977) and that the wings, when present, are restricted to the area below the distal widening of the proximal portion. The sporophyll of *Lepidophyllum jenneyi* White (1899, Pl. 59 Fig. 2) which shows very clearly the distally widened proximal portion was regarded as having lost its lateral wings while it was interpreted by Abbott (1963) as having a T-shaped pedicel and was transferred by this author to the genus *Lepidostrobus* (Fig. 8h). In *Lepidocarpopsis lanceolatus* (Lindley and Hutton) Abbott on the contrary, the pedicel is clearly alate, exceeding the width of the sporangium (Fig. 8i). The sporophylls of *Cyclostigma kiltorkense* Haughton (Fig. 8f) from the Upper Devonian of Ireland (Chaloner, 1968) and *Lepidostrobus bohdarowiczii* Bochenski (1936) from the Carboniferous of Poland (Fig. 8g) also have such a T-shaped pedicel and a long distal lamina, but their pedicel seems to be devoid of lateral wings. However, according to Taylor and Hickey (1992), the alation which characterizes the sporophylls of the arborescent lepidodendrids and those of the isoetaleans is a plesiomorphy and therefore is not phylogenetically informative.

THE TERMINOLOGY IN THE LYCOPSID REPRODUCTIVE ORGANS

Comparisons of the *Annalepis* sporophylls with those of the arborescent lycopsids and those of *Isoetes* underscore a problem of terminology. Indeed, as there is no standardization for the different groups of lycopsids, various terminologies occurred which make rather complex and confusing the comparative studies. As regards to the lepidodendrids, the proximal and distal portions of the sporophylls are respectively termed "pedicel" and "lamina" by most of the authors (Abbott, 1963; Chaloner, 1967; Emberger, 1968; Bateman et al. 1992; Stewart and Rothwell, 1993). Emberger (1968, p.179) noticed that the proximal portion is equivalent to a petiole bearing a sporangium. In contrast, Taylor and Taylor (1993, p.270) defined the lepidodendrid sporophylls (*Lepidocarpon* Scott) as consisting of two lateral laminae and a distal extension. The similarities between the *Annalepis* sporophylls and those of the lepidodendrids led Grauvogel-Stamm and Duringer (1983) to use for *Annalepis* the terminology applied to the latter by most authors. However the resemblances between *Annalepis* and *Isoetes* emphasized for the first time in this study, required to change the terminology employed previously, as it has been done above.

In contrast to the lepidodendrids, in *Isoetes* the proximal portion of the sporophyll is termed "vagina" while its distal portion is called "subula". The current use in the terminology of *Isoetes* of these Latin words has been introduced by Hickey (1985) whereas, previously, they were employed only in the Latin diagnosis (Braun, 1868; Duthie, 1929; Wanntorp, 1970). However the use of these Latin words complements those which were already in use for *Isoetes*, such as "ala", "ligula", "velum" and "labium". As for the lateral wings (or alae) which are present in the proximal portion of the *Isoetes* leaves, they are regarded as the restricted remnants of the lamina (Hickey, pers. com.). In fact the meaning of these Latin words describes the features of the different portions of the leafy sporophylls. Thus, the portion containing the alae is called "vagina" which means "sheath", because the wings are slightly enveloping, as shown for example in the drawings of Wanntorp (1970). On the other hand, as the distal outgrowth of the *Isoetes* sporophylls is awl-like shaped, it has been called "subula" which means "awl".

The terminology such as applied to *Isoetes* seems to be applicable to some of the Chinese species of *Annalepis* (Meng 1995, 1998, 2000), as noticed by Hickey (pers. com. 1999) who recognized a subula in some of them, but it does not seem applicable to all the *Annalepis*-like sporophylls, particularly those in which there is no subula. However, the leaf primordium of *Isoetes* also seems to be devoid of a subula. Thus, only the shape and growth sequence of the wings and the subula in young *Isoetes* leaves would allow to establish the exact homologies with *Annalepis* but this development has not yet been studied (Hickey, pers. com., September 1999).

CONCLUSIONS

The comparative analysis of the Triassic lycopsids *Pleuromeia* and *Annalepis* using new macromorphological and ultrastructural data provides signif-

icant support for their close relationship with each other and with the living genus *Isoetes* and more ancient lycopsids, some of which extend back to the Devonian.

A close affinity between *Pleuromeia* and *Annalepis* appears unquestionable. Preliminary observations of some rather well preserved specimens of *Annalepis* indicate that they have furrowed, bilaterally symmetrical rhizomorphs as in *Pleuromeia*. The sporophylls, with their adaxial sporangium and distal ligule, are comparable in both genera, except that the sporophylls of *Annalepis* are wedge-shaped and have well-marked membranous wings which are seemingly missing in *Pleuromeia*. Moreover, although they are monolete, the microspores of *Annalepis* clearly show the same ultrastructural features as the trilete microspores of *Pleuromeia*, i.e. a thin exospore with a thinner, non-folded apertural area combined with laminated zones, and a thicker spongy outer wall largely dissociated from the exospore and divided into two protruding lips above the aperture.

Most of the features shared by *Pleuromeia* and *Annalepis* also appear very similar to those of the living *Isoetes*. The comparative study of the rhizomorphs of *Pleuromeia* and *Isoetes* demonstrates that these organs have many points of structural and developmental correspondence. The ultrastructural features of the exospore and the spongy outer wall in the *Pleuromeia* and *Annalepis* microspores are remarkably similar and homologous with the walls of the *Isoetes* microspores (the latter having in addition a third, superficial wall, the perispore). This similarity between fossil and recent microspores is all the more striking because the fine structure of the *Isoetes* microspores differs markedly from that of all the other extant pteridophyte spores, including those of *Selaginella*. Indeed, despite some ultrastructural resemblances reflecting the relationships between *Isoetes* and *Selaginella*, the microspores of the latter show a number of unambiguous differences which strongly suggest that *Isoetes* is much more closely related to *Pleuromeia* and *Annalepis* than it is to *Selaginella*. The resemblances in morphology of the sporophylls also deserve to be noted. Snigirevskaya (1989) stressed the similarity between the sporophylls of *Pleuromeia* and the basal fertile region of *Isoetes* leaves. However, the clearly winged sporophylls of *Annalepis* show a stronger resemblance to *Isoetes*. In fact, the most important difference lies in the growth habit of the Triassic genera and that of *Isoetes*. Like some lycopsids from the Carboniferous (*Chaloneria cormosa*) and the Devonian (*Clevelandodendron ohioensis*), the Triassic lycopsids *Pleuromeia* and *Annalepis* have an elongated stem covered with entirely sterile leaves and a terminal, well-defined cone with short sporophylls, whereas the living genus consists of a short corm with long lacunate leaves, most of which bear a basal sporangium. However these differences do not seem to be very significant since they are rather common in the lycopsids where they are regarded as simple variations among related genera. The fact that in *Isoetes* many or all the leaves are fertile can be explained either by the loss of sterile leaves (Pigg, 2001) or, more likely, by the evolutionary reduction and transfer of the reproductive function to the vegetative leaves, as in the Gymnosperms and the Angiosperms (Nozeran, 1955).

All the similarities shown by both Triassic genera and *Isoetes* surely indicate close connections between them. Nevertheless, at first glance, they are not clearly indicative of a sister-group or an ancestor-descendant relationship and do not reveal the exact role played by *Pleuromeia* and *Annalepis* in the evolutionary history of *Isoetes*. However, there are some further noteworthy resemblances between *Annalepis* and *Isoetes* which strongly suggest that *Annalepis* is closer to the extant genus than *Pleuromeia* and that it is ancestral to *Isoetes*. Recently Meng (1998, 2000) also made this assumption. Besides their winged sporophylls/leaves noted above, there is, indeed, a striking similarity between the *Annalepis* sporophylls and the leaf primordia and scale leaves of the extant genus. Especially the scale-leaves which occur in many *Isoetes* species, and appreciably resemble *Annalepis* sporophylls, might be vestigial structures and might represent remnants of ancestral sporophylls, which might indicate that originally *Isoetes* had distinct sterile and fertile leaves as in *Pleuromeia* and *Annalepis*. The microspores of *Annalepis* are monolete as in *Isoetes,* whereas they are trilete in *Pleuromeia.* Moreover, the similarities between *Annalepis* and some Cretaceous and Tertiary fossils attributed to the genus *Isoetites* give further support to an ancestor-descendant relationship between *Annalepis* and *Isoetes.* The newly described species *Isoetites daharensis* from the Lower Cretaceous of Tunisia (Barale 1999), which is the best known among these plants, shows quite clearly that its sporophylls are remarkably similar to those of *Annalepis* and differ morphologically from the sterile leaves. Furthermore, its rhizomorph is cormose as in the Triassic genus, although not bilaterally symmetrical. As discussed above, *Isoetites horridus* from the Tertiary of North America (Brown 1939, 1958; Hickey 1977; Collinson 1991) was probably organized similarly, bearing its *Annalepis*-type sporophylls and sterile lacunate leaves in distinct areas, unlike *Isoetes.* These similarities strongly suggest that *Isoetites* and *Annalepis* are closely related and that *Isoetites* may have evolved from *Annalepis.* Thus the Triassic genus *Annalepis* seems to have played a more direct role in the evolutionary history of *Isoetes* than *Pleuromeia.* As regards to *Isoetites daharensis* and *I. horridus,* they may represent a group of lycopsids intermediate between *Annalepis* and *Isoetes,* and may indicate which structural changes occurred during this evolution. Thus the evolutionary series '*Annalepis—Isoetites—Isoetes*' appears very likely. Unfortunately, most of the *Isoetites* species are poorly known. They are usually identified on the sole basis of their lacunate leaves whereas the most important features, such as the precise shape and structure of the fertile parts and the microspore ultrastructure, remain unknown. The fine structure of *Minerisporites mirabilis,* the megaspore of *I. horridus* (Collinson, 1991), shows rather clearly the features of the isoetalean megaspores, but it does not provide any more precise informations on the affinities of *Isoetites.* Further and more thorough investigations of all the *Isoetites* material would be essential for definitely establishing the evolutionary series from the Triassic lycopsids to *Isoetes.* Besides, the fact that *Annalepis* and *Pleuromeia* are contemporaneous suggests that an ancestor-descendant relationship cannot exist between them. Therefore it is inferred that *Pleuromeia* either became extinct, or

originated within the nonalate species of *Isoetes*. However the latter hypothesis seems unlikely in view of the apparent homogeneity of the living genus which strongly suggests a monophyletic origin for it.

Some of the typical features of *Pleuromeia* and *Annalepis* are also present in more ancient lycopsids, providing some evidence of their ancestral affinities. The bilateral symmetry of the rhizomorph is known from the Devonian (Pigg, 2001). The sporophylls of the Carboniferous lepidodendrids, especially those with lateral wings, and those of more ancient lycopsids such as *Cyclostigma kiltorkense* from the Devonian of Ireland (Chaloner, 1968) are comparable in some respects to *Annalepis*. The special ultrastructural features of the microspores shared by the Triassic *Pleuromeia* and *Annalepis*, as well as by the extant *Isoetes*, also occur in *Polysporia* (Lugardon et al., 2000), *Chaloneria*, and other Carboniferous lycopsids. Moreover, it is of note that the trilete microspores of *Bisporangiostrobus harrisii* Chitaley and McGregor (1988) from the Upper Devonian of Pennsylvania contain proximal papillae as do the microspores of *Chaloneria/Polysporia*, *Annalepis*, *Pleuromeia* and *Isoetes*. This is all the more interesting since *Cyclostigma kiltorkense*, which has cones similar to those of *B. harrisii* (Stewart and Rothwell, 1993), also has a bilobed, bilaterally symmetrical rhizomorph as in *Pleuromeia*, *Annalepis* and *Isoetes*. Moreover several Frasnian-Famennian (Late Devonian) dispersed spores have ultrastructural characteristics comparable to those of the microspores of the Triassic genera and the extant genus (unpublished observations, B.L.). Thus it appears that the main features characterizing the rhizomorph and the microspores of living *Isoetes* appeared very long ago and remained outstandingly unchanged from the Devonian to the present. It is likely that these features characterize a particular group among the rhizomorphic lycopsids and that this group probably has a very remote origin. However, this group cannot be defined at the present time, notably because there are no accurate data on the microspore ultrastructure of most of the fossil lycopsids, mainly the arborescent lepidodendraleans. Methodical fine studies of in situ microspores of these lycopsids would surely supply significant information on the origin, relationships and delimitation of the different groups of isoetalean lycopsids.

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